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Early Pleistocene small mammals from Marathoussa, a new locality in the Mygdonia basin, Macedonia, Greece

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The fossiliferous site of Marathoussa (Mygdonia basin, Macedonia, Greece) is located in the Platanochori Formation, which consists mainly of lacustrine sediments. The site includes one level with micromammals and several levels with fresh-water mollusks. The micromammalian fauna contains several species of insectivores and rodents. The faunal elements suggest an early Pleistocene age. Detailed morphological and metrical comparisons of the arvicolids allow the dating of the fauna to the early Biharian and, more precisely, to the Betfia Phase.

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INTRODUCTION

The paleontological and stratigraphical research in the Mygdonia basin started at the beginning of the eighties by a team led by Prof. G.D. Koufos. Since then, several fossiliferous sites have been found, while a great amount of fossils has been unearthed. This material has been studied and, besides two Ph.D. theses, a number of papers have been published (for the bibliography see Koufos & Kostopoulos 1997). A new fossiliferous site including mammals and mollusks was found in 1994 by one of the authors (G.E.S.); the locality is named Marathoussa (MAR). Our first collection from the various beds of Marathoussa section indicated the presence of a rich micromammalian fauna in one of them. Collecting was continued until 1997 and the collected fossils are described in the present article.

The material has been measured on a Zeiss Stereoscope (Dept of Biology, University of Thessaloniki) and on a Reflex Microscope 3-D (Dept of Geology, University of Utrecht). Measurements are given in mm, unless something else is indicated. The nomenclature and the way of measuring of the Soricidae are given in Reumer (1984), of the Muridae in Van de Weerd (1976) and Martin Suarez & Freudenthal (1993) respectively, of the Cricetidae in Mein & Freudenthal (1971) and Daams & Freudenthal (1988) respectively, of the Arvicolidae in Van der Meulen (1973), of the Sciuridae in De Bruijn (1966) and Van de Weerd (1976), of the Zapodidae in Green (1977). All the material is stored in the Laboratory of Geology and Palaeontology, University of Thessaloniki.

GEOLOGY AND STRATIGRAPHY

The Mygdonia basin is an east to west-north-west trending inland tectonic depression in the area of Central Macedonia, Greece. The pre-Neogene basement consists of crystalline, mainly metamorphic rocks of the Circum Rhodope belt and the Serbomacedonian massif, as well as granitic rocks. The Neogene-Quaternary sedimentary deposits of the basin were divided in two Groups, the Premygdonian and the Mygdonian Group. The Premygdonian Group corresponds to the time interval from the Middle Miocene to the Early Pleistocene. During the ?Middle Miocene an inland tectonic depression (the Premygdonian basin) was formed and gradually filled up by fluvial, continental, lacustrine and fluvio-lacustrine clastic sediments up to ~350 m thick (Psilovikos 1977). The Premygdonian Group has been divided in three formations: the Chrysavgi, Gerakarou, and Platanochori Formations, respectively (Koufos *et al.* 1995).

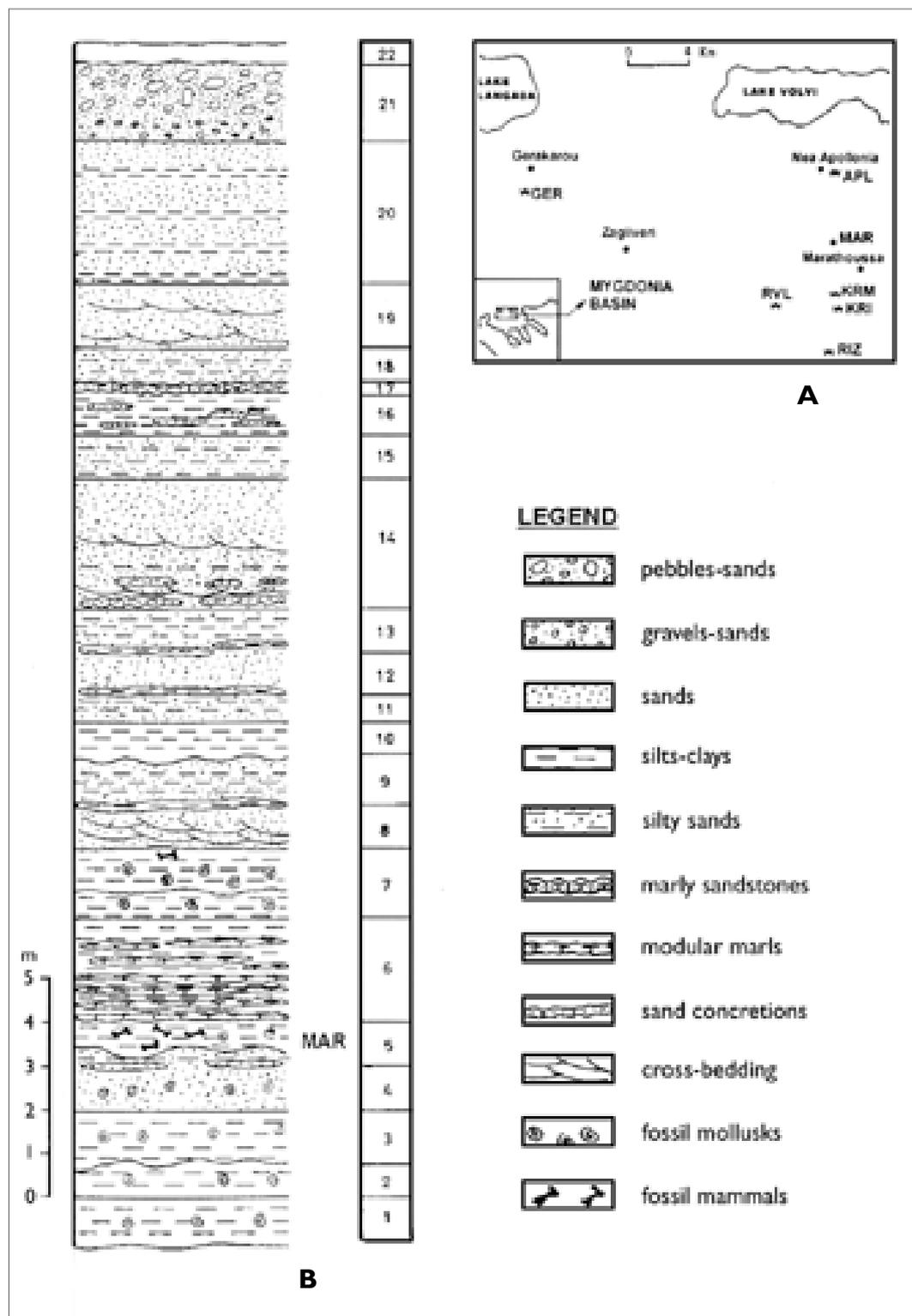
The Mygdonian Group was deposited during the Middle Pleistocene to Holocene. During the end of the Early Pleistocene, a new inland tectonic depression (the Mygdonia basin) was formed into the central part of the former Premygdonian basin. The new basin was filled up with fresh water and an extensive lake (Mygdonia lake) was formed. Mygdonia lake gradually dried up and the present lakes of Koronia and Volvi are the relics of it. Lacustrine and fluvio-lacustrine sediments up to ~150m thick were deposited during the

Middle Pleistocene to Holocene, forming the Mygdonian Group. Several fossiliferous sites have been recognized in the basin. The fossiliferous sites include macro- and micro-mammalian fossils and fresh-water mollusks (Koufos *et al.* 1992, Koliadimou 1996, Kostopoulos 1996). The fossil faunas are rich and allowed the dating of the formations. The Chrisavgi Formation is the oldest one and has been dated to the end of the Middle Miocene (end MN 7+8). The upper part of the Gerakarou Fm has been dated to Late Pliocene - Early Pleistocene and the Platanochori Fm to the end of the Early Pleistocene (Koufos & Kostopoulos 1997).

LOCALITY

The locality of Marathoussa is situated 3 km NW of the village of Marathoussa, in the Mygdonia basin (Fig. 1A). The locality is situated in the Platanochori Fm, which consists mainly of lacustrine deposits. The Marathoussa site is close to the locality of Apollonia (APL) (Koufos *et al.* 1992). A stratigraphical correlation of the two sections is not possible, due to a very dense network of faults. The locality includes a rich micro-mammalian fauna in the bed 5, while there are several beds with fresh-water mollusks (Fig. 1B). The mollusks were unknown in the Mygdonia deposits. The first indication about their presence comes from the locality of Apollonia (Koufos *et al.* 1992). The Marathoussa molluscan fauna includes the following species: Gastropoda: *Valvata* sp., *Bithynia* sp., *Lymnaea* sp., *Planorbis* cf.

Figure 1 **A.** Sketch map of Mygdonia basin with the fossiliferous sites. **B.** Stratigraphical column of the Marathoussa section. Lithostratigraphical legend of the beds: **22.** Soil; **21.** Sand with subangular quartzitic pebbles; **20.** Greyish sands with intercalations of grey-green silts and clays; **19.** Yellowish coarse cross-bedded sands; **18.** Grey-green silty sand; **17.** Grey marly sandstone; **16.** Grey-green silt/clay with nodules of grey marly sandstone; **15.** Grey-greenish silty sand; **14.** Grey-greywhite coarse cross-bedded sands with small sandstone concretions in the lower part; **13.** Brownish grey silty sand; **12.** Grey coarse sand with gravels; **11.** Grey thin bedded silty sand; **10.** Brownish grey massive silt/clay; **9.** Grey-yellowish silty sand; **8.** Grey cross-bedded coarse sands with gravels, more dark coloured at the base; **7.** Brownish green silt/clay with numerous fragments of fresh-water mollusks; **6.** Intercalations of thin (5-20cm) beds of grey nodular marl with dark grey-green massive silt/clay. Four marly intercalations appear in the lower part; **5.** Brownish-black silts/clays with numerous fragments of micromammals and fresh-water mollusks; **4.** Grey-greenish fossiliferous (mollusks) fine silty-clayey sands. In the upper part there are nodules of marly sandstone; **3.** Brown silt/clay with fresh-water mollusks; **2.** Brownish green silty-clayey sands with mollusks; **1.** Grey-green silt/sand with mollusks.



planorbis, *Planorbis* sp., *Armiger* aff. *crista*, *Gyraulus* aff. *albus*, *Segmentina* sp., *Acroloxus* sp. *Bivalvia*: *Pisidium* sp., pearly fragments of Unionidae indet., Ostracodes indet., in addition to Charophytes indet. and calcareous fragments of egg shells, probably of birds. The lithostratigraphy of the Marathoussa section is given in Fig. 1B

SYSTEMATIC PALAEOLOGY

Order: Insectivora BOWDICH, 1821

Family: Talpidae GRAY, 1825

Subfamily: Desmaninae THOMAS, 1912

Desmaninae indet.

Material:

P4, 1 sin.: 130.

M1, 2 dex.: 35, 117. 1 sin.: 493.

M2, 2 dex.: 503, 510. 1 sin.: 525.

M3, 3 dex.: 504, 524, 526.

p2, 1 dex.: 551.

p3, 3 sin.: 133, 550, 552.

p4, 1 dex.: 487.

m1, 1 sin.: 42.

m2, 1 sin.: 486.

m3, 2 dex.: 40, 456. 2 sin.: 41, 39.

Mandible: 484, 487.

Measurements: see Tables 1 and 2.

Description:

P4 (Plate 1, 1): It is strongly molarized and sub-triangular in shape. The paracone is high and the posterocrista starting from it lacks a metacone, bends slightly to the lingual side and ends to the postero-lingual cingulum. On the other hand, the anterocrista is extremely weak and ends to the parastyle. The lingual lobe is very pronounced, with the anterior side concave and the posterior one straight. The protocone is rather high and well separated from the paracone. The postero-lingual basin is shallow and narrow, bordered by a strong cingulum, which lacks a hypocone. There is a very small postero-labial basin bordered by a weak cingulum, while in the anterior part of the tooth the cingula are almost absent.

M1 (Plate 1, 2): The metacone and paracone

are very high, separated by a deep valley. The parastyle is well developed, separated from the paracone and connected with the protoconule through a weak cingulum. The protoconule is connected with the protocone, with which it is of equal size, and the paracone through a low ridge. The posterocrista of the protocone bears an elongated accessory cusp, which is separated from the metaconule.

There is a weak cingulum running along the posterior edge of the molar, starting from the metaconule and ending next to the posterior arm of the metacone. The metastyle is absent. The labial side of the tooth bears a weak cingulum, while the lingual side lacks one.

M2 (Plate 1, 3): The posterior arm of the metacone ends slightly more labially than the anterior arm of the paracone. The parastyle is a small widening on the antero-labial cingulum. The cusps are as on the M1, except for the protocone and the protoconule that are separated. The cingulum that runs along the anterior part of the tooth, from the protoconule to the parastyle, is strong, while the one in the posterior edge of the tooth is reduced only in the postero-labial corner. The cingula along the labial and the lingual side are absent. The lingual side of the tooth is slightly assymetrical, due to the anterior position of the protocone.

M3: The parastyle is absent; there is a weak cingulum anteriorly to the parastyle. The protoconule is small, connected with the paracone by an anterior and a posterior ridge and separated from the protocone. There is a small, elongated accessory cusp on the posterocrista of the protocone and a deep valley separates it from the metaconule. The metaconule and the metacone are separated. In one specimen there is a valley lingually to the accessory cusp and a small cusplule in it. The lingual lobe is rather prominent in one specimen.

p2: It has an elliptical shape. A very weak paraconid is present. There is a well developed cingulum in the postero-lingual side that forms a small bulge in the posterior corner, in the base of the posterocristid.

p3: There is a small paraconid in two specimens, while in the third it is absent. The anterocristid is well pronounced, while the posterocristid is less pronounced. There is a small bulge at the base of the posterocristid. The well pronounced posterior cingulum curves upwards and forms narrow basins postero-lingually and postero-labially, with the postero-lingual one wider.

p4 (Plate 1, 4a & b): The lingual margin is straight, while the labial one is strongly convex. The anterocristid ends near the antero-lingual corner, where a paraconid is formed. A narrow talonid basin is present. The posterocristid is very weakly developed and at its end a small hypoconid is formed. The entoconid is absent. There is a narrow cingulum running along the antero-labial side of the tooth.

m1 (Plate 1, 5a & b): The morphology of the tooth is very simple. The oblique cristid ends on the metaconid. The entostylid is small and independent. There is a weak and narrow cingulum starting from a very small cuspid in the re-entrant valley, running labially to the trigonid and along the anterior part of the tooth and ending before the parastyle, which is very small. The cingula along the lingual and posterior part of the tooth and labially to the talonid are absent.

m2: The morphology is very similar to that of the m1. The antero-labial cingulum extends far to the antero-lingual corner of the tooth, where the parastylid is formed.

m3: (Plate 1, 6): The cusps are as on the m1,2; so are the cingula, only weaker. The oblique cristid ends on the protoconid-metaconid crest. The entostylid and the cuspid in the re-entrant valley are extremely small, while the parastylid is bigger.

Discussion: Rümke (1985) gave some characteristics of the subfamily Desmaninae. The p4 often bears a metaconid or a metaconal rib; the oblique cristid of the lower molars ends either against the tip of the metaconid or against the protoconid-metaconid crest; the m3 is slightly reduced; the upper molars have a divided mesostyle and a strongly developed

lingual part featuring a protoconule, a protocone, a metaconule and often a small tubercle on the posterocrista of the protocone. All these features are present in the Marathoussa sample. The genera included in the subfamily are: *Desmana*, *Galemys*, *Dibolia* (= *Ruemkelia*) and *Mygalinia* (Rümke 1985). The genera are distinguished mainly on the basis of morphological features of the incisors and the premolars and two ratios, p2/p3 and P2/P3. The scantiness of the material and the absence of these teeth from the Marathoussa sample makes the identification of the genus to which the sample belongs impossible.

Family: Soricidae FISCHER VON WALDHEIM, 1817

Subfamily: Crocidurinae MILNE-EDWARDS, 1872

Genus: *Crocidura* WAGLER, 1832

***Crocidura kornfeldi* KORMOS, 1934**

Material:

I sup., 7 dex.: 33, 383, 388, 395, 397, 401, 404. 6 sin.: 382, 387, 392, 405, 429, 576.

P4, 4 dex.: 541, 542, 544, 546. 2 sin.: 153, 540.

A1 sup., 5 dex.: 556, 558, 560, 563, 564. 3 sin.: 557, 561, 562.

A2,3 sup., 1 dex.: 546. 4 sin.: 574, 580, 581, 582.

M1, 4 dex.: 490, 495, 508, 544. 1 sin.: 507.

M2, 7 dex.: 45, 498, 499, 506, 511, 518, 519.

4 sin.: 48, 496, 497, 514.

M3, 1 sin.: 536.

I inf., 1 dex.: 426. 4 sin.: 412, 413, 415, 423.

A1 inf., 2 dex.: 559, 569. 2 sin.: 566, 575.

p4, 6 sin.: 472, 475, 570, 571, 572, 573.

m1, 5 dex.: 448, 453, 468, 470, 473. 7 sin.: 109, 432, 454, 455, 471, 472, 475.

m2, 6 dex.: 54, 452, 468, 470, 473, 476. 4 sin.: 457, 461, 462, 474.

m3, 2 dex.: 464, 476. 3 sin.: 465, 474, 555.

Measurements: see Tables 3 and 4.

Description:

I sup. (Plate 2, 13a & b): There are seven complete specimens which can be described. The apex is single (the incisor is not fissident). The cingulum along the postero-buccal margin is narrow but well pronounced, while the antero-buccal part of the cingulum is strong and undulate.

A sup. (Plate 2, 14a & b): The upper antemolars are typical for *Crocidura*, triangular, with a crest directed from the main cusp to the distal part of the tooth. The cingula are wide and well pronounced. The A1 is larger than the other two antemolars.

P4 (Plate 2, 15): The parastyle is separated from the paracone by a deep valley. The protocone is small and situated buccally in the antero-lingual corner. The hypocone is not a distinct cusp, but it forms a cingulum-like ridge that runs along the lingual margin of the tooth. The hypoconal ridge is separated from the protocone by a valley. The posterior emargination is strong.

M1 and M2 (Plate 2, 16 & 17): They are both relatively broad and short and with slender cusps. The protocone is connected to the paracone, while between the protocone and the metacone there is a wide and deep valley. The hypocone is situated postero-lingually to the protocone. The valley that separates the hypocone from the protocone is rather shallow. In the M1 the posterior emargination is strong. In one of the M1s, there is a small cuspule situated lingually to the protocone.

M3 (Plate 2, 18): It is relatively short. The protocone and the hypocone form a ridge that surrounds the lingual basin. The protocone is the best developed cusp.

I inf. (Plate 2, 19a & b): The apex is curved upwards. The upper margin of the two teeth that are complete is slightly bicuspluate in the first and tricuspluate in the second. The buccal cingulum is narrow but well pronounced. Along the lingual face of the incisor there is a groove that curves downwards below the notch in the basal border.

A inf. The lower antemolars are typical for *Crocidura*, with two low crests, beginning

from the main cusp and directed the one postero-lingually and the other postero-buccally. The cingula are wide and strong, but the buccal one stops before the anterior end of the tooth.

p4 (Plate 2, 20): The lower premolar has one high and pointed cusp. Both the lingual and the buccal cingula are strong and wide.

m1 and m2 (Plate 2, 21): The buccal re-entrant valley opens in a large distance above the base of the molars. The entoconid crest is rather low. The buccal cingulum is very narrow, the lingual one is wider and they are both undulate and not well pronounced.

m3 (Plate 2, 22a & b): The talonid consists only of the hypoconid and, thus, does not form a basin. The buccal cingulum is narrow and well pronounced, but the lingual one is very weak and it disappears completely under the talonid.

Mandible: The mandibles, which were found, consist only of the horizontal ramus that is high but narrow. The mental foramen is placed underneath the posterior part of the p4.

Discussion: The presence of one triangular cusp on the p4, the position of the mental foramen underneath the posterior-most part of the p4 and the unpigmented teeth lead to the assumption that the specimens from Marathoussa belong to the subfamily Crocidurinae. Several genera are included in this subfamily. According to Repenning (1967), the genus *Crocidura* is characterised by a reduced talonid with hypoconid only on the m3, short lower incisor with upturned apex, occlusal surface without cuspules and a groove along the lingual length that curves downward below the notch in the basal border. All these characters have been recognized in the Marathoussa teeth, which must be identified as *Crocidura*.

A number of species are included in the genus *Crocidura*. The Marathoussa sample will be compared to those found in Southeastern Europe. The recent species *C.*

russula (HERRMANN, 1780) is characterised by the constriction in the buccal cingulum of the m2 (Reumer 1996). The absence of this feature from the m2s of Marathoussa teeth differentiates the latter from *C. russula*. A species of *Crociodura* described only from the Pleistocene of Crete (Xeros) is *C. zimmermanni* (WETTSTEIN, 1953). The P4 from Xeros has broader lingual basin with a more-developed protocone situated more lingually and larger distance between the parastyle and the paracone than the P4 from Marathoussa. The lower incisor from Xeros is much larger, with more pronounced buccal cingulum than that from Marathoussa. The lower molars from Xeros have a weaker lingual cingulum than those from Marathoussa (pers. observation). Therefore, the Marathoussa sample does not belong to *C. zimmermanni*.

The species *C. kornfeldi* was described by Kormos (1934) and its diagnostic features are: the P4, M1 and M2 that are relatively short and broad, the upper molars that have a short degree of posterior emargination and the lower incisor that is acuspluate. Some more dental characters of the species are the buccal position of the protocone in the P4 and the presence of a narrow and undulate cingulum in the lower molars. The presence of these characters in the teeth of Marathoussa allow us to determine the sample to this species. The *C. kornfeldi* from Marathoussa is morphologically identical to that from Ravin Voulgarakis (Koliadimou 1996) and that from Osztramos 3/2 (Reumer 1984). Moreover, the dimensions of the teeth from the three localities are very similar (Fig. 2).

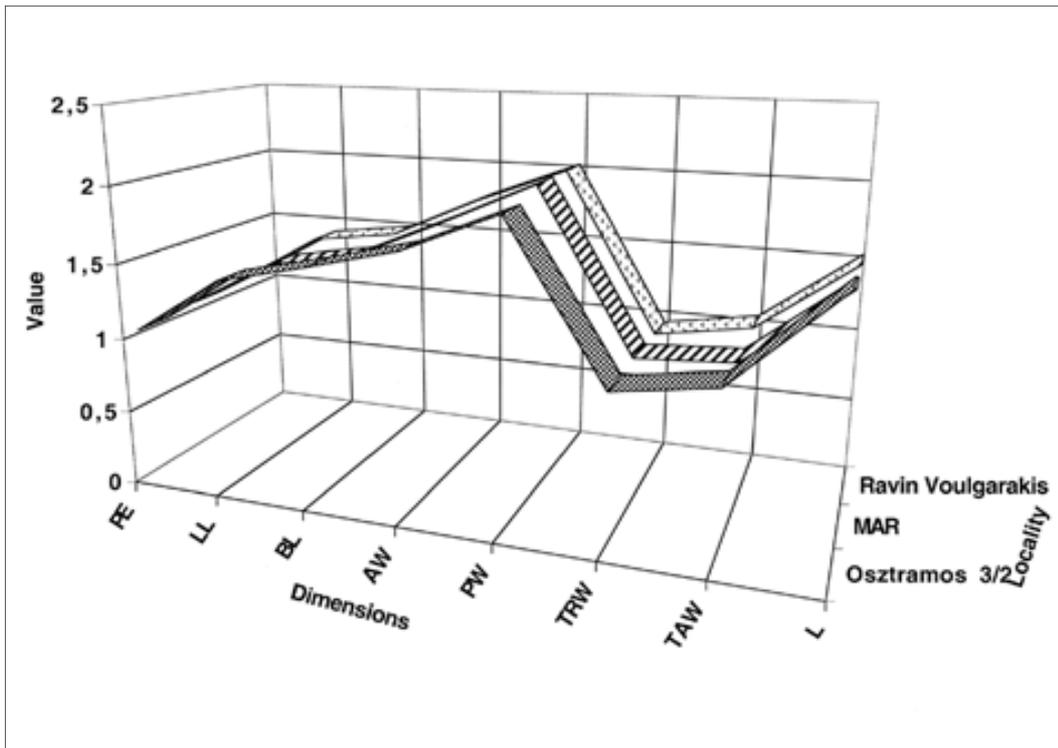


Figure 2 Diagram with the mean values of the dimensions for the M1 (PE, LL, BL, AW, PW) and the m1 (TRW, TAW, L) of three samples of *C. kornfeldi* from Osztramos 3/2 (Reumer, 1984), Ravin Voulgarakis (Koliadimou, 1996) and Marathoussa.

Subfamily: Soricinae FISCHER VON WALDHEIM, 1817

Tribe: Soricini FISCHER VON WALDHEIM, 1817

Genus: *Sorex* LINNAEUS, 1758

***Sorex minutus* (LINNAEUS, 1766)**

Material:

I sup., 3 dex.: 396, 406, 407. 7 sin.: 32, 124, 125, 389, 398, 399, 402.

P4, 2 sin.: 89, 113.

M1, 1 dex.: 101. 5 sin.: 46, 505, 509, 515, 516.

M2, 1 dex.: 99.

I inf., 3 dex.: 128, 419, 425. 3 sin.: 410, 414, 417.

m1, 1 dex.: 444. 3 sin.: 53, 110, 459.

m2, 4 dex.: 431, 442, 443, 460. 5 sin.: 100, 107, 439, 441, 449.

m3, 1 dex.: 106.

Mandible, 1 sin.: 480.

Measurements: see Tables 5 and 6.

Description:

I sup. (Plate 2, 1a & b): All specimens are fissident. The talon is very large and pointed. There is a buccal cingulum in all of the complete incisors.

P4 (Plate 2, 2): The hypocone corresponds to a small elevation of the lingual cingulum, while a wide valley separates it from the protocone. The protocone is situated buccally and bears a short crest directed posteriorly that forms a small cuspule postero-lingually to the parastyle. The parastyle is connected to the paracone by a rather high parastylar crest.

M1 and M2 (Plate 2, 3): The metaloph is divided in two branches: the first is connected to the metacone and the second is directed posteriorly, but stops buccally to the hypocone. The latter is small and situated on the lingual cingulum, which starts from the postero-lingual corner of the molar and stops right under the protocone. The hypocone is separated from the second branch of the metaloph by a deep valley.

I inf. (Plate 2, 4a & b): Two of the six available specimens are complete. They are both

tricuspluate, but a very small prominence is formed posteriorly to the last cuspule, so that it gives the impression that they are tetracuspluate. The central valley is the deepest of the three existing. There is a rather wide but not well-pronounced cingulum on the buccal posterior margin of four specimens. There is also a weak cingulum along the lingual posterior margin in all the incisors.

m1 and m2 (Plate 2, 5a & b, 6a & b): The entoconid is situated posteriorly and the entoconid crest is very high. The oblique crest bears a mesoconid on the unworn specimens. The buccal re-entrant valley opens in small distance above the buccal cingulum. The latter is narrow but well pronounced, while the lingual cingulum is wide but not pronounced. **m3**: The talonid consists of a well formed basin with hypoconid, entoconid and entoconid crest. The cingula are like in the other lower molars.

Mandible: One fragment of the horizontal ramus was found. It is short and narrow and the distance between the alveoli shows rather small molars. The area of the mental foramen is absent.

Discussion: The high entoconid crest on the m1,2 and the basined talonid of the m3 characterise the genus *Sorex* (Repenning 1967). Their presence in the studied material allow its classification to this genus. Several species are included in the genus *Sorex*. The presence of the fissident upper incisors, however, characterises only two Eurasian species: *S. minutus* and *S. mirabilis* HOFFMANN, 1971. Also, in *S. araneus* a fissident upper incisor may occasionally be observed (Reumer 1985), but not always as in the assemblage from Marathoussa. The teeth from Marathoussa differ from *S. mirabilis* mainly because of their smaller size. On the other hand, they have the same morphology as, and a size very close to, those of *S. minutus* from Tegelen described by Reumer (1984). Their morphology is also identical to the morphology of the teeth of *Sorex* cf. *minutus* from Ravin Voulgarakis (Koliadimou 1996), but

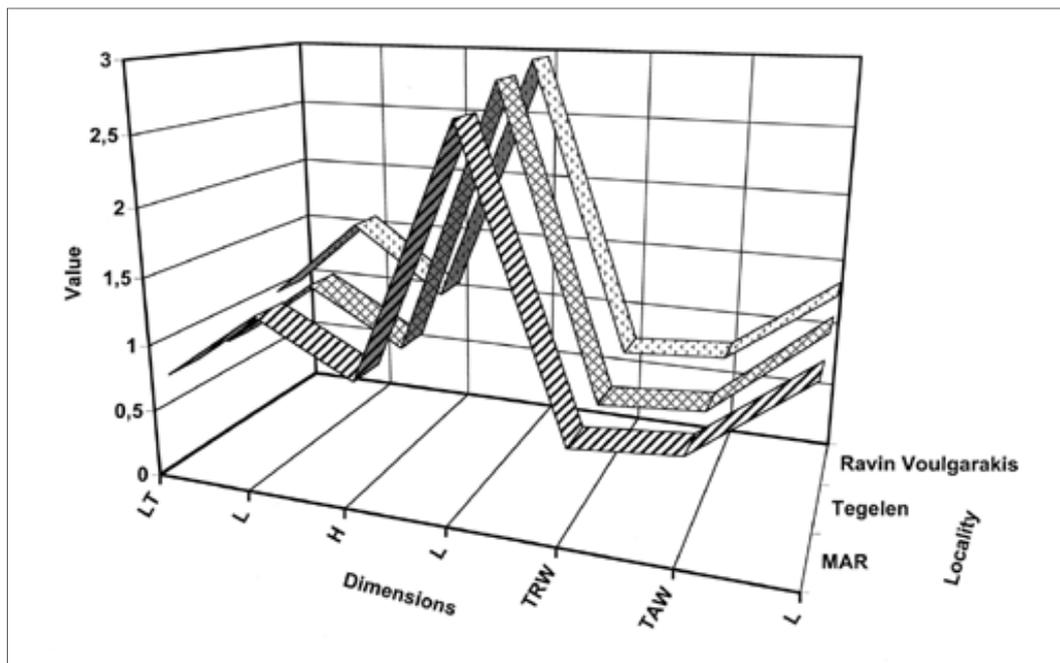


Figure 3 Diagram with the mean values of the dimensions for the I sup (L, LT, h), the I inf (L) (TRW, TAW, L) of *S. minutus* from Tegelen (Reumer 1984) and Marathoussa and *S. cf. minutus* from Ravin Voulgarakis (Koliadimou 1996).

the size of the latter is larger (Fig.3). All these allow us to determine the Marathoussa sample as *Sorex minutus*.

Genus: *Sorex* LINNAEUS, 1758
 Subgenus: *Drepanosorex* KRETZOI, 1941
Sorex (Drepanosorex) praeearaneus
(KORMOS, 1934)

Material:

I sup., 7 dex.: 386, 393, 394, 400, 403, 408, 428. 5 sin.: 122, 123, 384, 385, 390.
 A sup., 12 dex.: 579, 583, 585, 586, 587, 588, 590, 600, 601, 602, 603, 604. 2 sin.: 584, 589.
 P4, 3 dex.: 50, 118, 543. 3 sin.: 115, 116, 539.
 M1, 2 dex.: 501, 530. 1 sin.: 520.
 M2, 2 dex.: 43, 97. 6 sin.: 44, 47, 49, 102, 451, 502.
 M3, 1 dex.: 533. 3 sin.: 535, 537, 538.
 I inf., 2 dex.: 34, 421. 4 sin.: 129, 154, 409,

424.
 A1, 1 sin.: 565.
 p4, 1 dex.: 549. 5 sin.: 135, 136, 137, 138, 547.
 m1, 1 dex.: 52. 5 sin.: 51, 438, 445, 447, 469.
 m2, 3 dex.: 52, 434, 435. 6 sin.: 51, 436, 450, 467, 477, 527.
 m3, 2 dex.: 105, 466. 4 sin.: 51, 114, 463, 469.
 Mandibles, 3 dex.: 52, 479, 481. 7 sin.: 51, 467, 469, 477, 482, 483, 485.

Measurements: see Tables 7 and 8.

Description:

I sup. (Plate 3, 1a & b): It is fissident. The talon is well developed and sharply pointed. The five complete specimens show a very broad, undulated cingulum along the buccal posterior margin.
A sup. (Plate 3, 2): The upper antemolar is bulbous. The buccal and the lingual cingulum

are strong. In nine of the studied teeth there is a ridge connecting the lingual cingulum with the main cusp, on the antero-lingual part of the tooth. The postero-lingual basin is wide.

P4 (Plate 3, 3): The two complete specimens have a very weak hypocone, separated from the protocone by a wide valley that is lingually surrounded by a small cingulum. A cingulum starts from the protocone, directed towards the parastyle. In five of the specimens, it continues under the latter. On this cingulum, lingually to the parastyle, there is a small cuspule on all the specimens.

M1 and M2 (Plate 3, 4 & 5): None of the available teeth can be certainly identified as M1. However, there are three fragments, which are described as M1, because they are slightly larger than the complete molars, which are identified as M2. All teeth (complete and broken ones) have a weakly developed hypocone, separated from the protocone by a valley. In the lingual side of this valley there is a cingulum. The metaloph is not well developed and between the latter and the metacone there is a wide and deep valley.

M3 (Plate 3, 6): The hypocone and the metacone are united forming a ridge, on the posterior part of the tooth, which is separated from the protocone by a valley. On the lingual margin of the valley there is a small cingulum which seems to be an extension of the ridge and stops lingually to the protocone.

I inf. (Plate 3, 7a & b): Three of the studied teeth are complete. They are all tricuspluate with well developed, bulbous cuspules. There are three valleys separating the cuspules from each other and the middle one is the deepest. There is no sign of cingulum on the buccal side.

A1 inf. (Plate 3, 8a & b): The a1 found is only slightly smaller than the p4. It is also bulbous and the cingula on both the lingual and the buccal sides are wide but not pronounced. A postero-lingual basin is almost distinguishable.

p4 (Plate 3, 9a & b): The tooth is bulbous

with lingual and buccal cingula. The postero-lingual basin is wide and, in three out of five specimens, bordered postero-lingually by a short ridge.

m1 and m2 (Plate 3, 10a & b): The entoconid is situated posteriorly, while the entoconid crest is rather high. On some unworn specimens the oblique crest forms a small mesoconid. The buccal re-entrant valley opens in a small distance above the cingulum. The lingual cingulum is wide but not well projected, while the buccal one is narrower, well developed and undulate.

m3 (Plate 3, 10a & b): The talonid forms a wide basin with a well-developed hypoconid and entoconid and a high entoconid crest. The cingula are as on the m1 and the m2.

Mandible (Plate 3, 11a & b): There is one complete hemi-mandible found, in the assemblage from Marathoussa. The apex of the coronoid process is rounded. There is a coronoid spicule situated very close to the apex. The external temporal fossa is very shallow, with not very distinct borders and reaches the upper condylar facet. The upper and the lower facets of the condyle are almost parallel and the interarticular area is relatively broad all along the condyle. The internal temporal fossa is triangular and extends far upwards to the apex of the coronoid process. The mental foramen is preserved in four fragments and is situated under the p4/m1 transition, on three and under the middle of the m1, on the fourth of them.

Discussion:

Drepanosorex is considered as a subgenus of the genus *Sorex* and is characterised by generally robust teeth, slightly to strongly exoedodont anterior dental elements, a comparatively large condyle and fissident upper incisors (Reumer 1985). The presence of all these features in the Marathoussa sample allows its determination to *Drepanosorex*. The subgenus includes the following species: *D. praeareneus* KORMOS, 1934, *D. margaritodon* KORMOS, 1930, *D. savini* HINTON, 1911 and

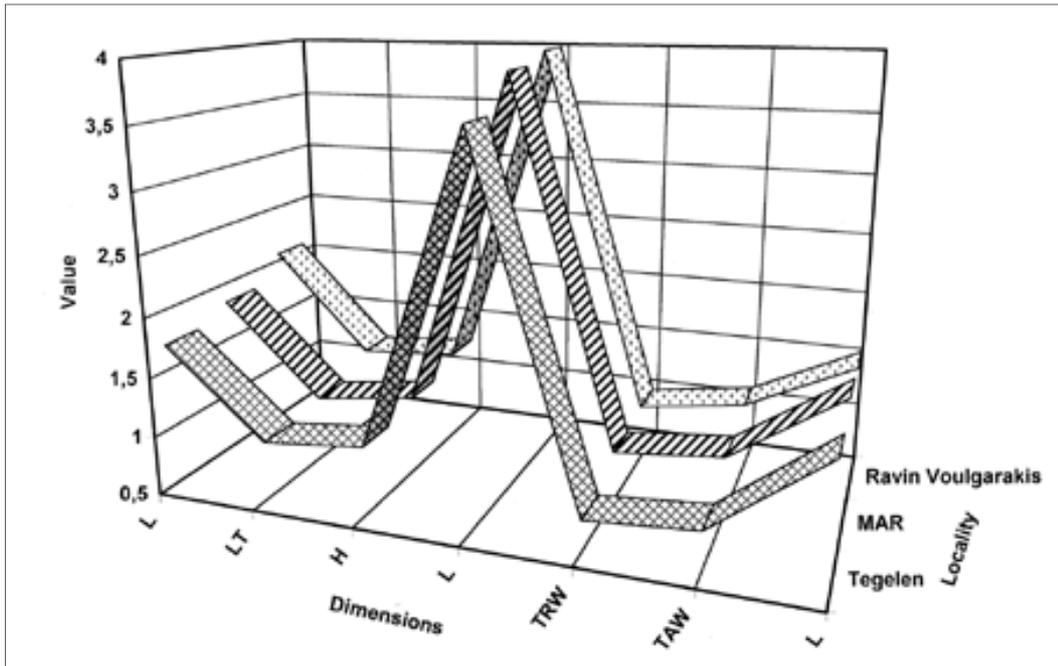


Figure 4 Diagram with the mean values of the dimensions for the I sup (LT, L, H), the I inf (L) and the m I (TRW, TAW, L) of *D. praeareaneus* from Tegelen (Reumer 1984) and Marathoussa and *D. cf. praeareaneus* from Ravin Voulgarakis (Koliadimou 1996).

D. austriacus KORMOS, 1937, while *D. pachyodon* PASA, 1947 and *D. tasnadii* KRETZOI, 1941 are considered to be synonymous to *D. praeareaneus* and *D. savini*, respectively.

According to Reumer (1984), the species of *Drepanosorex* form a morphological sequence with three trends: increase of exoedaeodonty, size increase and enlargement of the condyle. The presence of a slight exoedaeodonty in the antemolars and the small (comparatively to the other species) size of the teeth from Marathoussa, indicate that they belong to *D. praeareaneus*, the most primitive species of *Drepanosorex* known. The mean values (Fig. 4) of the dental dimensions from Marathoussa are slightly higher than those from Tegelen (Reumer 1984) and lower than those from Ravin Voulgarakis (Koliadimou 1996).

Tribe: Neomyini MATSCHIE, 1909

Genus: *Asoriculus* KRETZOI, 1959

***Asoriculus gibberodon* (PETENYI, 1864)**

Material:

I sup., 3 dex.: 119, 120, 391.

M1, 6 dex.: 95, 96, 103, 437, 488, 513. 2 sin.: 494, 521.

M2, 1 dex.: 517. 2 sin.: 491, 512.

M3, 2 dex.: 104, 534. 1 sin.: 532.

I inf., 1 sin.: 422.

m1, 3 dex.: 440, 446, 458. 1 sin.: 111.

m2, 1 dex.: 433. 1 sin.: 108.

Measurements: see Tables 9 and 10.

Description:

I sup. (Plate 2, 7a & b) : Only one upper incisor is complete and it is fissident. The talon is rather short. There is a well-developed and undulate cingulum on the postero-

buccal margin of the tooth.

M1 and M2 (Plate 2, 8 & 9): The hypocone is well developed and separated from the protocone by a valley. On the lingual part of this valley there is a cingulum. In one specimen, this cingulum forms a cuspule lingually to the protocone. The hypocone is also separated from the ridge that surrounds the hypoconal flange by a very shallow valley. The metaloph is present and, in four specimens, it is divided in two, small branches. The anterior margin of the molars bends strongly beside the protocone. The parastyle is very strong.

M3 (Plate 2, 10): The protocone and the paracone are well developed, while the metacone forms a ridge on the posterior margin of the tooth. The hypocone is united to this ridge, but is very short. There is a cingulum running along the lingual margin of the molar.

I inf. (Plate 2, 11a & b): One broken lower incisor was found in Marathoussa. The dorsal margin shows a deep valley and another one, shallower, situated anteriorly to the first. The tooth, thus, is bicuspluate. The apex is upturned. The posterior part of the tooth is not preserved.

m1 and m2 (Plate 2, 12a & b): The entoconid crest is very low, but present. The oblique crest bears a mesoconid in the unworn specimens. The buccal re-entrant valley opens in a very small distance above the cingulum. The buccal cingulum is narrow, undulate and well pronounced, the lingual one is wide and less pronounced.

Discussion:

The short and bicuspluate lower incisors, the broad but not pronounced lingual cingulum of the lower molars in the Marathoussa sample allow us to recognise the genus *Asoriculus*. The genus includes only European fossil species dated from latest Miocene/Earliest Pliocene (Doukas *et al.* 1995) to the Middle Pleistocene (Koliadimou 1996). These species were described as *Episoriculus*, together with the recent species from Asia. However,

Hutterer (1994) distinguished the European fossil species as belonging to *Asoriculus*, while the Asiatic recent ones belong to *Episoriculus*. The species of *Asoriculus*, therefore, are: *A. gibberodon* (PETENYI, 1864), *A. castellarini* (PASA, 1947), *A. tornensis* JANOSSY, 1973, *A. borsodensis* JANOSSY, 1973 and *A. thenii* MALEZ & RABEDER, 1984. The species *A. tornensis* and *A. borsodensis* are now considered as synonyms of *A. gibberodon* (see Reumer 1984).

The characteristic of *A. thenii* that differentiates this species from the assemblage from Marathoussa is its longer I inf. with strongly upturned apex. The species *A. castellarini* was initially described by Pasa (1947) as *Neomys castellarini*, based on material from Cava Sud (Soave, Italy). Later on, *A. cf. castellarini* has been reported from Monte Peglia 63 (Orvieto, Italy) (van der Meulen 1973), from Vcelare 3,4 a/7 (Slovakia) (Fejfar & Horacek 1983) and from Ravin Voulgarakis (Greece) (Koliadimou 1996). The type material is scanty and not well preserved. The samples from Monte Peglia 63 and Ravin Voulgarakis are also scanty and fragmentary. The species shares a lot of features in common with *A. gibberodon*, including the size of the dental elements. Some differences seem to be in the area of the mandibular articulation. In *A. cf. castellarini* from Ravin Voulgarakis the coronoid process inclines somewhat anteriorly, the interarticular area is narrow and the internal temporal fossa extends upwards. In *A. cf. castellarini* from Monte Peglia 63 the coronoid process inclines backwards, the interarticular area is lingually deeply excavated and the internal temporal fossa extends upwards without reaching the tip of the coronoid process. Finally, in *A. cf. castellarini* from Slovakia, the coronoid process is anteriorly inclined. The variability in the morphology of the mandibular articulation within the species *A. castellarini* is not well defined. On the other hand, in *A. gibberodon* the interarticular area is also narrow, the coronoid process has concave margins

and the internal temporal fossa continues upwards to just below the tip of the coronoid process. The distinction of the two species based on the morphology of the mandibular articulation is not clear and needs further study, which might lead to their synonymy (Reumer 1984).

The species *A. gibberodon* is reported from several localities in Europe (Table 11). There is a large variability in the morphology of the upper molars, which have been separated in two morphotypes within the species (Reumer 1984). Morphotype A is characterised by an isolated hypocone, separated by a small valley from the ridge that surrounds the hypoconal flange. Morphotype B has a hypocone that is considerably less developed and connected to the ridge surrounding the flange. The PE-index, calculated by means of the formula $[(LL+BL)/2*PE]-1$ (Reumer 1984), is a number between 0 and 1: higher values of the index indicate larger degree of posterior emargination. For Morphotype A, the PE-index is moderate, while for Morphotype B, the index is moderate to strong. Despite the variability in the morphology of the upper molars, the lower molars do not show any variability. However, size differences are also observed among the dental remains from the various localities. There is not any relation between the size of the morphotypes and time (in Osztromos 7 both morphotypes were found) and these differences cannot be used for biostratigraphical correlation.

The fissident upper incisors, the bicuspluate lower incisors, as well as the low entoconid crest and the buccal re-entrant valley opening slightly above the cingulum in m1,2s indicate that the Marathoussa sample can be attributed to *A. gibberodon*. The morphology of the upper molars suggests similarities to Morphotype A. The mean value of the PE-index for the M1s is 0.18 and for the M2s 0.14 (Tab. 11), which also confirm the similarity. The Marathoussa teeth are larger than

those described from some European localities (Tab. 12), but they have the same size as *A. gibberodon* from Tourkovounia 1 (Reumer & Doukas 1985) (based on comparison of the two assemblages).

Tribe: Beremendiini REUMER, 1984

Genus: *Beremendia* KORMOS, 1934

***Beremendia fissidens* (PETENYI, 1864)**

Material:

P4, 1 dex.: 545. 1 sin.: 139.

M1, 1 dex.: 545. 1 sin.: 489.

M2, 1 dex.: 492.

M3, 1 sin.: 531.

m1, 1 sin.: 478.

Mandible, 1 sin.: 478.

Measurements: see Table 13.

Description:

P4 (Plate 1, 7): It is almost triangular, with a low protocone, situated close to the parastyle, while the hypocone is placed anteriorly.

Between the protocone and the hypocone there is a very shallow valley. The parastyle is large, with a high parastylar crest.

M1 and M2 (Plate 1, 7 & 8): The protocone is situated on a U-shaped crest, which connects it to both the paracone and the metacone. The hypocone is low and separated from the protocone by a deep valley.

M3 (Plate 1, 9): The M3 is rather reduced, in relation to the other upper molars. The protocone is low and situated lingually. The lingual margin is circular. The hypocone is a cusp separated from the protocone by a shallow valley. The crest between the paracone and the metacone is vertical to the crest that connects the paracone and the parastyle.

m1 (Plate 1, 10a & b): The trigonid basin is deep and wide due to a slight posterior-ward shift of the metaconid. The entoconid crest is short. The lingual cingulum is slightly developed, but the buccal one is well developed and a little undulate.

Mandible (Plate 1, 10b): On the fragment of

one mandible with the m1 the mental foramen is situated underneath the buccal re-entrant valley of the first molar.

Discussion: The tribe Beremendiini includes only the genus *Beremendia*. Kormos (1934) did not give a formal diagnosis for it, but he gave descriptions for the diagnostic dental elements of the genus (I sup., upper antemolars, I inf. and m3). Unfortunately, in the Marathoussa samples these teeth were not found. However, the slight posterior-ward shift of the metaconid in the m1s and m2s, in relation to other genera, is characteristic for the genus (Reumer 1984). The morphology of the m1 found in Marathoussa shows this character. Furthermore, the size of the studied teeth falls within the limits of variation for the teeth of the genus *Beremendia*. Therefore, the specimens from Marathoussa belong to this genus.

Four species of the genus *Beremendia* have

been described: *B. ucrainica* (PIDOPLICHKO, 1956), *B. minor* RZEBIK, 1976, *B. sinensis* (ZDANSKI, 1928) and *B. fissidens* (PETENYI, 1864). The species *B. ucrainica* is considered synonymous to *B. fissidens* (Rzebik-Kowalska 1976). The species *B. minor* is similar to the specimens from Marathoussa, but the size of its elements is much smaller.

The species *B. sinensis*, originally described as *Neomys sinensis*, was later transferred to *Beremendia* (Kretzoi 1956). The elements are only slightly smaller than those of *B. fissidens* and the main difference between the two species is in the area of the mandibular condyle. Unfortunately, there is no homologous feature in the Marathoussa mandible for comparison. The dental morphology of the studied teeth is identical to that of *B. fissidens* from Ravin Voulgarakis, Tegelen and Monte Peglia 63 (Koliadimou 1996; Reumer 1984; van der Meulen 1973). However, the dimensions of the Marathoussa M1 and m1

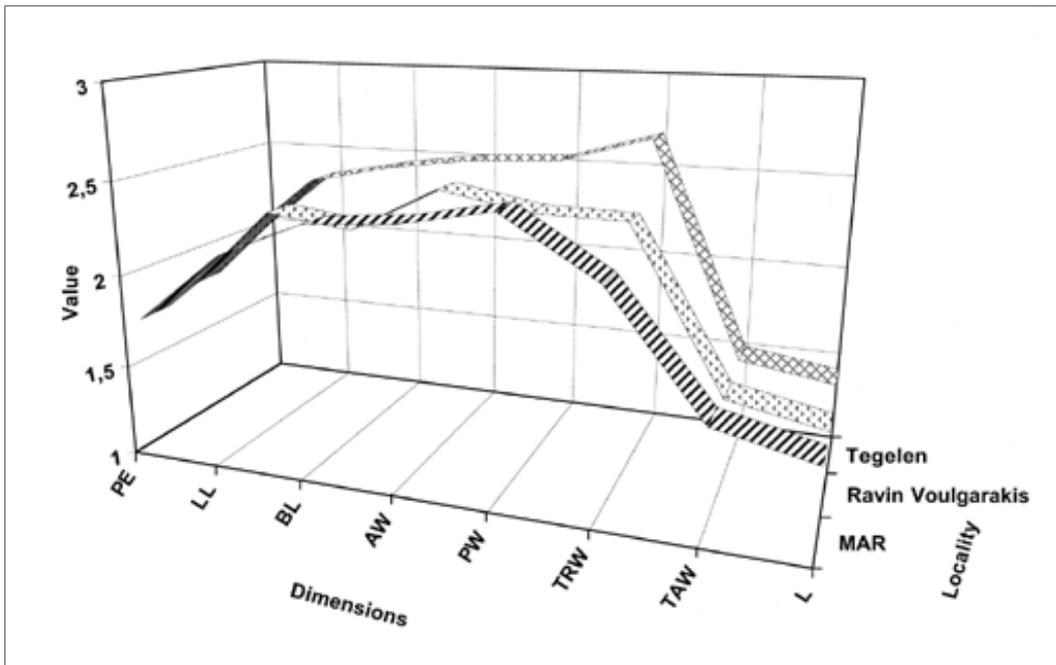


Figure 5 Diagram with the mean values of the dimensions for the M1 (PE, LL, BL, AW, PW) and the m1 (TRW, TAW, L) of three samples of *B. fissidens* from Tegelen (Reumer 1984), Ravin Voulgarakis (Koliadimou 1996) and Marathoussa.

are smaller than those of Tegelen and larger than those of Ravin Voulgarakis (Fig. 5). Taking into account all the above mentioned, the Marathoussa sample of *Beremendia* must be attributed to *B. fissidens*.

Order: Rodentia BOWDICH, 1821

Family: Sciuridae GRAY, 1821

Subfamily: Marmotinae POCOCK, 1923

Tribe: Citellini GROMOV, 1965

Genus: *Spermophilus* CUVIER, 1825

***Spermophilus* sp.**

Material:

P4, 1 dex.: 156.

M1-2, 1 dex.: 378. 1 sin.: 381.

m3, 1 dex.: 379.

Measurements: see Table 14.

Description:

P4: The only tooth found is broken and worn. Only the protocone can be distinguished, which is very prominent.

M1-2 (Plate 4, 1): The shape of the tooth is triangular. The protocone is the most prominent cusp. It is connected with the paracone and the metacone by two low ridges. So, the main cusps form a V on the occlusal surface. There are no metaconule or protoconule. The mesostyle is very well-developed. There is a cingulum running along the anterior margin of the tooth. The posterior cingulum starts from the mesostyle, ends next to the metacone and is less pronounced than the anterior cingulum. The roots are not preserved.

m3 (Plate 4, 2): The anterior width is larger than the posterior one. The protoconid is very strong, while the metaconid and the hypoconid are rather well-developed and connected with the protoconid through the anterior lop-hulid and the ectolophid, respectively. There are no endoconid or mesostylid. The occlusal surface is closed and a wide basin. is formed in the middle. The roots are not preserved.

Discussion: The Sciuridae from Marathoussa are scanty. However, the triangular shape of the M1-2, the same size of the paracone and the metacone and the low posterior cingulum on the M1-2, the large width relatively to the length and the shape of the mesoconid on the m3 indicate similarities to the genus *Spermophilus*. The genus *Spermophilus* includes several recent and fossil European species with small differences. The main differences are referred to the number of the roots and the morphology of the premolars.

In the material from Marathoussa the roots are not preserved and no premolars were found. The molars from Marathoussa resemble to those from Ravin Voulgarakis (Koliadimou 1996), which belong to the species *S. nogaici*. However, the M1-2 from Marathoussa are larger than those from Ravin Voulgarakis and the m3 from Marathoussa is smaller than that from Ravin Voulgarakis. Moreover, the absence of metaconule and protoconule and the presence of the mesostyle distinguish them from the RVL sample. The scanty material from Marathoussa cannot allow certain comparisons for a specific determination and, thus, it is referred as *Spermophilus* sp.

Family: Zapodidae COUES, 1875

Subfamily: Sicistinae ALLEN, 1901

Genus: *Sicista* GRAY, 1827

Sicista* cf. *subtilis

Material: m1 dex.: 597.

Measurements: L=1.147; W=0.896

Description:

m1 (Plate 4, 3): The only molar that was found is very worn and the morphological features are not well distinguished. There is a rather large anteroconid that is united to the protoconid and the metaconid. There is not a mesostylid or ectostylid, while the mesoconid is very low. The posterior cingulum is low and ends on the endoconid.

Discussion: The molar found in Marathoussa belongs to the genus *Sicista*, which is characterised by brachyodont molars with simple morphology. According to Kowalski (1979), *Sicista* is separated in two evolutionary branches. The first is represented by the species *S. betulina*, with a rather complicated morphology on the molars, and the second by the species *S. subtilis*, with very simple morphology. The molar from Marathoussa, with a simple morphology, belongs to the second group, which first appeared in Pliocene of Asia, with the species *S. pliocaenica*. In Greece and the Balkan region only representatives of the second branch have been reported. The molar from Marathoussa is quite similar, in morphology and size, to the molar from Arnissa (Mayhew 1977) that was classified as *S. subtilis*. The same species was also reported from Ravin Voulgarakis (Koliadimou 1996), with upper molars so that comparison between the two samples is impossible. The sole specimen of Marathoussa and its simple morphology allow us to determine this as *S. cf. subtilis*.

Family: Muridae GRAY, 1821

Genus: *Apodemus* KAUP, 1829

Apodemus sylvaticus/flavicollis

Material:

M1, 7 dex.: 28, 142, 191, 193, 194, 195, 223.

7 sin.: 143, 144, 192, 196, 197, 198, 222.

M2, 10 dex.: 147, 148, 149, 199, 200, 223,

354, 356, 357, 368. 3 sin.: 201, 202, 224.

M3, 5 dex.: 152, 349, 355, 370, 374. 2 sin.:

151, 224.

m1, 8 dex.: 25, 146, 204, 205, 206, 208, 358,

369. 10 sin.: 145, 203, 207, 209, 210, 211,

259, 360, 361, 362.

m2, 5 dex.: 215, 219, 220, 363, 364. 6 sin.:

212, 213, 214, 216, 217, 218.

m3, 4 dex.: 155, 221, 350, 367. 8 sin.: 351,

352, 353, 365, 366, 371, 372, 373.

Measurements: see Table 15.

Description:

M1 (Plate 4, 4 & 5): The tooth is oval. The t1 is situated posteriorly of the t3 in 27% of the teeth and it is always connected with the t2. In one specimen there is a t1 bis and in three specimens there is a t2 bis. In eight specimens the t1 and the t5 are connected through a spur, in three the t1 bears a smaller spur towards the t5 and in one specimen the t1 does not bear a spur. In six specimens the t3 is connected with the t5 and in five specimens the t3 bears a small spur. In nine specimens the t7 and t4 are separated, while in the remaining three (25%) the two cusps are connected with each other. The t7 is relatively large and oval. The t4 and the t6 are almost symmetrical. The t12 is very small in all the specimens. It is connected with the t8, but not with the t9 in eight specimens and it is connected with the t8 and t9 in two specimens. The t9 is smaller than the t6 and it is connected with the t8 in eight out of eleven specimens. There are four roots.

M2 (Plate 4, 6 & 7): The length and the width are almost equal. The t1 is almost triangular and bears a small spur in two out of nine specimens. The t3 is small, without a posteriorly directed spur. The t7 is large and it is connected with the t4 only in four out of ten specimens. The t9 is smaller than the t6, but still relatively large in 70% of the teeth. The t12 is very small, almost absent. The t9 and the t8 are connected in all the teeth.

There are four roots.

M3: The t1 is big and oval and isolated in the two unworn specimens. In the rest the t1-t5-t4 and t5-t6-t8 are connected. There are three roots.

m1 (Plate 4, 8-10): The antero-lingual and the antero-labial cuspids (a.lg.c. and a.lb.c. respectively) are symmetrical in 92.3% of the teeth. The antero-central cuspid (a.c.c.) is small in nine and absent in two specimens, while it is large in the remaining three specimens. It is connected with the a.lg.c. and the

a.lb.c. except for one specimen. There is a large posterior accessory cuspid (c1) connected with the hypoconid; in front of it there are one (41.7%) or two (58.3%) smaller accessory cuspids on the labial cingulum. The terminal heel is low. It is rounded in eight and elongated in five specimens. There is a small spur directed from the hypoconid-entoconid junction towards the protoconid-metaconid junction in twelve specimens, while the longitudinal crest is well developed only in three specimens.

m2: It is almost square. The a.lb.c. is large only in one out of eleven specimens. It is elongated and connected with the protoconid by a low ridge in the anterior edge of the tooth. The c1 is very reduced in all teeth and absent in two specimens. Only one specimen has a second accessory cuspid on the labial cingulum. There is a short longitudinal spur in six specimens; the spur is even shorter in the remaining five teeth and it is never connected with the protoconid-metaconid junction. The terminal heel is low, elongated and almost of equal size as, or a little smaller than, the a.lb.c..

m3: The tooth is triangular. Half of the specimens preserve a small a.lb.c., but in the other half of them it is absent. In three out of eleven specimens there is a very small posterior cuspid (c1).

Discussion:

The presence of the t7 and the t12, the connection of the t6 with the t9, the anterior position of the t1 and its connection with the t2 in all studied M1s, the presence of the a.c.c., the tendency of the cuspid pairs to form chevrons and the rareness of longitudinal spur in the m1s of the Marathoussa sample are characteristic for the genus *Apodemus*. The genus includes many species and the Marathoussa material will be compared to some European and Western Asian species of approximately the same size only.

Apodemus dominans KRETZOI, 1959 is a well-

known European species that differs clearly from the Marathoussa sample, by the following features: its M1 has large posterior cingulum and three roots, its M2 has a large t9 and the t1 lacks a posteriorly directed spur, its m1 has a mostly elongated posterior cingulum and weak accessory cuspids on the labial cingulum. Moreover, *A. dominans* teeth are slightly larger than those of the Marathoussa sample (Table 16).

Apodemus caesareanus BATE, 1942, known from the Middle-East, has many similarities with the specimens from Marathoussa, including their size (Tab. 16), but also some features that clearly distinguish it from the Marathoussa *Apodemus*. In the M1 of *A. caesareanus*, the t1 and the t4 are of equal size and smaller than the t7, the t2 bis is absent and a fifth root is very common. In the M1 from Marathoussa the t7 is smaller than the t1 and the t4, the t2 bis is present in three out of eleven molars and there are always four roots. The buccal cingulum in the m2 of *A. caesareanus* has three distinct, well-developed cuspids, whereas the m2 from Marathoussa have a very weak cingulum. In the m3 of *A. caesareanus* both a.lb.c and posterior cuspid exist, but in the m3 from Marathoussa the a.lb.c. exists in six and the posterior cuspid in three out of eleven molars. Therefore, the *Apodemus* from Marathoussa does not belong to this species.

Another species known from Middle-East is *Apodemus levantinus* BATE, 1942. The m1 of this species is longer (Tab. 16) and the M2 has a much larger t1 than those from Marathoussa. The m1 and m2 of this species have a very well-developed labial cingulum with four cuspids. On the contrary, the m1 and m2 from Marathoussa have a weak cingulum with two or three cuspids in the m1 and one or none in the m2. Finally, in the m3 of *A. levantinus* a posterior cuspid is common in most cases, but in the m3 of Marathoussa this cuspid is very rare. The above morpholo-

gical and metrical differences distinguish the Marathoussa sample from *A. levantinus*.

Apodemus atavus HELLER, 1936 from Gundersheim-4 (Germany) has three roots, the t12 is slightly smaller than the t7 and the t4 is situated posteriorly and is always connected with the t7. The M2 has a t12, the t4 and t7 are connected and the t3 is rather big. The t9 has the same size as the t12 and is not connected with the t8. The m1 has a very large a.c.c. that is always connected with the a.lb.c. and a.lg.c.. The buccal cingulum is well developed, with two or three cusps. The protoconid and the metaconid are connected with the anterior cusps. There is a longitudinal spur, but there is no connection between the two posterior chevrons. The terminal heel is round and has the same size as the a.c.c. The m2 has a well developed buccal cingulum with two cusps. The a.lb.c. and the terminal heel are of equal size, rather large. The m3 has a well pronounced a.lb.c.. The molars of *A. atavus* are very close metrically to those of Marathoussa (Tab. 16). However, the very small t12 and the four roots on the M1, the absence of the t12 from the M2, the very small a.c.c. on the m1, the weak buccal cingulum on the m2 and the very small or absent a.lb.c. on the m3 of the Marathoussa sample differentiate the latter from *A. atavus*.

Apodemus etruscus ENGESSER, 1989 is a primitive species of *Apodemus*, with almost similar dental dimensions to the recent *A. sylvaticus* (Tab. 16). In 40% of the M1s the t7 is absent, while all M2s have a small t7. The t6 and t9 are not connected in 30% of the M1s and in 33% of the M2s. The M1 and M2 have three roots. All the m1s have a well-developed a.c.c.. Most of the m2s have three accessory cusps on the labial cingulum. In all these features, the specimens from Marathoussa differ from *A. etruscus*. M1s and M2s always have a well developed t7, the t6 is always connected with the t9, and

they have four roots, the a.c.c. in the m1s is small or absent and most of the m2s have one cingulum cuspid only. These differences indicate that *A. etruscus* is much older than the Marathoussa sample.

Two of the extant species of *Apodemus* that are found in Western Anatolia are *A. hermonensis* FILIPPUCI *et al.*, 1989 and *A. uralensis* PALLAS, 1811. The first species has an M1 in which both the t1 and the t3 are connected with the t5 and, thus, the tooth is somewhat stephanodont. A t1 bis is usually present. On the M2 the t1 is large and, in most cases, has an anterior and a posterior connection with the t5. On the m1 the buccal cingulum is well developed and the a.c.c. is usually isolated from the a.lb.c. and the a.lg.c.. The M1 from Marathoussa, however, show no tendency to develop stephanodonty and a t1 bis is rarely present. On the M2 the t1 has not two connections with the t5, the buccal cingulum of the m1 is less developed and the a.c.c. is usually connected with the a.lb.c. and the a.lg.c.. Therefore, the Marathoussa *Apodemus* differs from *A. hermonensis*, even though they share many common features. The second species, *A. uralensis*, is characterized by a ridge-like t7 on the M1 and M2, a t1 mostly separated from the t2 on the M1, a well-developed a.c.c. and an asymmetrical posterior chevron (the entoconid is displaced anteriorly) on the m1. On the M1 and M2 from Marathoussa, the t7 is a well-developed cusp and the t1 and t2 are always connected. On the m1, the a.c.c. is rather small and the posterior chevron is almost symmetrical. Thus, the specimens from Marathoussa cannot be identified as *A. uralensis*.

Many extant *Apodemus* species differ in exterior appearance, but their dental elements are similar. The specimens from Marathoussa belong to either *A. sylvaticus* or *A. flavicollis*, two species which are found both fossil and extant all over Europe. In *A. flavicollis* (MELCHIOR, 1834) the t1 of the M1 is placed

posteriorly and the t4 and t7 are rarely connected to each other; the t1 of the M2 has very often a posteriorly directed spur and the t12 is very reduced or absent; the m1 has a very reduced or small a.c.c. and the longitudinal spur is frequently well-developed, to such an extent that the two chevrons are connected with each other; the labial cingulum on the m2 is reduced (Pasquier 1974). In *A. sylvaticus* (LINNAEUS, 1758) the t1 and t3 on the M1 are symmetrical and placed at equal distances from the t4-t6 line, the t4 and t7 are often connected; on the M2, the t1 is triangular and rarely bears a posteriorly directed spur and a t12 is mostly present; on the m1 the a.c.c. is rather large and the longitudinal spur is weakly developed (Pasquier 1974). All the other characters of the dentition of the two species are the same and identical to those from Marathoussa. There seems to be also a small difference in the size of the two dentitions, as *A. flavicollis* has a little larger dental elements. However, a comparison of fossil and extant samples from Eurasian localities (Table 17), indicates that the size of the two species varies chronologically and geographically, in such a way that no trends can be detected. The size difference is small and overlaps, even in the recent samples. The teeth from Marathoussa show a mixture of the characters of *A. sylvaticus* and *A. flavicollis* and cannot be identified at the species level with certainty; therefore, we refer to them as *A. sylvaticus/flavicollis*.

Family: Cricetidae ROCHEBRUNE, 1883
 Subfamily: Cricetinae MURRAY, 1886
 Genus: *Cricetinus* ZDANSKY, 1928
Cricetinus koufosi KOLIADIMOU, 1996

Material:

M1, 1 dex.: 345. 2 sin.: 346, 347.
 M2, 1 dex.: 29. 2 sin.: 348, 380.
 M3, 1 dex.: 375. 1 sin.: 376.
 m1, 1 dex.: 150.
 m2, 2 dex.: 30, 377.

Measurements: see Table 18.

Description:

M1 (Plate 4, 11): The anterocone consists of two well-developed, separated cusps. There is a not very pronounced anterior cingulum, which forms a small pre-anterocone in one specimen; the third specimen is very worn and the features of this area are not clear. There is an anterolophule that connects the anterior cusps to the protocone. On the two unworn molars there is a very small spur labially to the anterolophule directed towards the paracone, but not connected with it. The entolophe connects the protocone and paracone to the hypocone. The metacone is connected with the posterolophe through a very short metalophule. The posterolophe is well-developed and, thus, the hypocone and metacone are united on the posterior part of the tooth and the posterosinus is closed. The lingual cingulum is absent, while the labial one is present but not well pronounced. In one specimen, there is a small parastyle. The labial sinuses are wider, but the lingual ones are deeper. There are four roots.

M2 (Plate 4, 12): The morphology is very similar to that of the M1. The protocone is united to the paracone through an anterior and a posterior ligament and so does the hypocone to the metacone. The posterolophe is well developed and the posterosinus is closed. The posterior metalophule is absent. The cingula are not very prominent. There are four roots.

M3: The dental pattern is similar to that of the M2, but the paracone is very weak, the tooth has a triangular shape. The labial cingulum is very strong. There are three roots.

m1 (Plate 4, 13): The only m1 found is very worn. The anterior margin is smooth, without cingulum and convex. The anteroconid is separated in two small cuspidids. The anterolophid is underdeveloped (does not emerge from the level of the anterosinusid) and connects the antero-labial cuspidid to the metaconid. The protoconid is united to the ento-

conid through the ectolophid. The posterolophid is well-developed and reaches the postero-lingual margin of the tooth. The posterosingulus is closed. The labial sinuses are wide and the labial and lingual cingula are well-developed. There are two roots.

m2: The morphology is similar to that of the m1, but the molar is wider. The labial anterolophid is well-developed, while the lingual one is absent. There are two roots.

Discussion: The genus *Cricetinus* has an m1 with undivided or slightly divided anteroconid, a smooth and convex oral surface, missing mesolophid and a very low, I-shaped anterolophid, while the upper first and second molars are characterised by missing or weakly developed mesolophids and the M2 rarely bears a posterior metalophule (Hir 1997). The presence of these features in the Marathoussa sample suggest a determination to the genus *Cricetinus*.

The species in this genus are: *C. varians* (ZHENG, 1984), *C. gritzai* (TOPACHEVSKI & SKORIK, 1992), *C. europaeus* (KRETZOI, 1959), *C. beremendensis* HIR, 1994 and *C. koufosi* KOLIADIMOU, 1996. *C. varians* is known from the Middle Pleistocene of China. The m1 of this species and of the Marathoussa sample have approximately the same size, while all the other molars of this species are larger than their homologous from Marathoussa (Figs. 5-9). The M1 of *C. varians* lacks a preanterocone and the m2 usually has a mesolophid (Zheng 1984).

The species *C. gritzai* was described from Odessa, Ukraine (Topachevski & Skorik, 1992). The large size (Figs. 5-9), the rare presence of the preanterocone and the very small metalophule in M1, the well-developed anterolophid of m1, as well as the presence of a mesolophid - always in m1 and usually in m2 - distinguish this species from the Marathoussa *Cricetinus*.

The species *C. europaeus* was described from Csarnota 2 (Kretzoi 1959). The M1 always lacks an anterior cingulum or preanterocone, while the M1s found in Marathoussa have either an anterior cingulum or a preanterocone. The M2 of *C. europaeus* sometimes has a mesolophid, which is absent in the Marathoussa M2. The posterior part of the M2 from Csarnota 2 is less wide than the anterior part. On the M2 from Marathoussa the two parts have equal width. On the m1 of *C. europaeus* the anteroconid is not always divided in two, and the anterolophid is higher than the one on the m1 from Marathoussa. Finally, the m2 of *C. europaeus* usually bears a mesolophid, which is absent from the Marathoussa one. The dental dimensions of *C. europaeus* are rather close to those of Marathoussa (Figs. 5-9). However, the morphological differences cannot allow the determination of the Marathoussa sample to *C. europaeus*.

The dental morphology of the Marathoussa *Cricetinus* resembles that of *C. beremendensis* from Hungary (Hir 1994). However, the teeth from Marathoussa are slightly larger than those from Beremend 15, the type locality of that species (Figs. 6-10). Furthermore, there are some small differences in the morphology that separate the two samples. On the M1 of *C. beremendensis* the metacone is always connected with the posteroloph without a metalophule, while on the M1s from Marathoussa there is a metalophule through which the metacone and the posteroloph are connected. On the m1 from Marathoussa the posterosingulus is broader than that of the m1 from Beremend 15. Finally, on the m2 from Marathoussa the buccal anterolophid is better developed than that from Beremend 15. Thus, the material from Marathoussa differs from *C. beremendensis*.

The dental features of the Marathoussa sample are similar to those of *C. koufosi*, described by Koliadimou (1996), from Ravin Voulgarakis. According to her descriptions, the M1 has a

preanterocone, a metalophule, a rare parastyle and a mesoloph or a spur labially to the anterolophule. The m1 has an anteroconid divided in two cusplids rather high above the roots, a very low, I-shaped anterolophid and no mesolophid. The presence of all these features on the molars from Marathoussa indicates similarities with *C. koufosi*. All the molars from Marathoussa have approximately the same size as those from Ravin Voulgarakis (Figs. 6-10). Thus, the Marathoussa sample is here described as *C. koufosi*.

Family: Arvicolidae GRAY, 1821

Subfamily: Arvicolinae GRAY, 1821

Tribe: Arvicolini KRETZOI, 1955

Genus: *Mimomys* FORSYTH MAJOR, 1902

Mimomys sp.

Material:

M2, 1 sin.: 240.

M3, 1 sin.: 611.

Measurements:

M2: L=2.05, W=1.15

M3: L=2.20, W=1.15

Description:

M2 (Plate 5, 1): It consists of the AL1, T2, T3 and T4. The enamel-free areas are on the buccal and the lingual side of the AL1 and on the posterior edge of the T4. The enamel is thinner on the posterior sides of the triangles and thicker on the anterior ones ("*Mimomys*-type"). The synclines are closed at the base of the tooth and there is abundant crown-cement in the BRA1, BRA2 and the LRA2. There is a *linea sinuosa* very low under the crown, but the roots are absent.

M3 (Plate 5, 2): It consists of the AL1, T2,

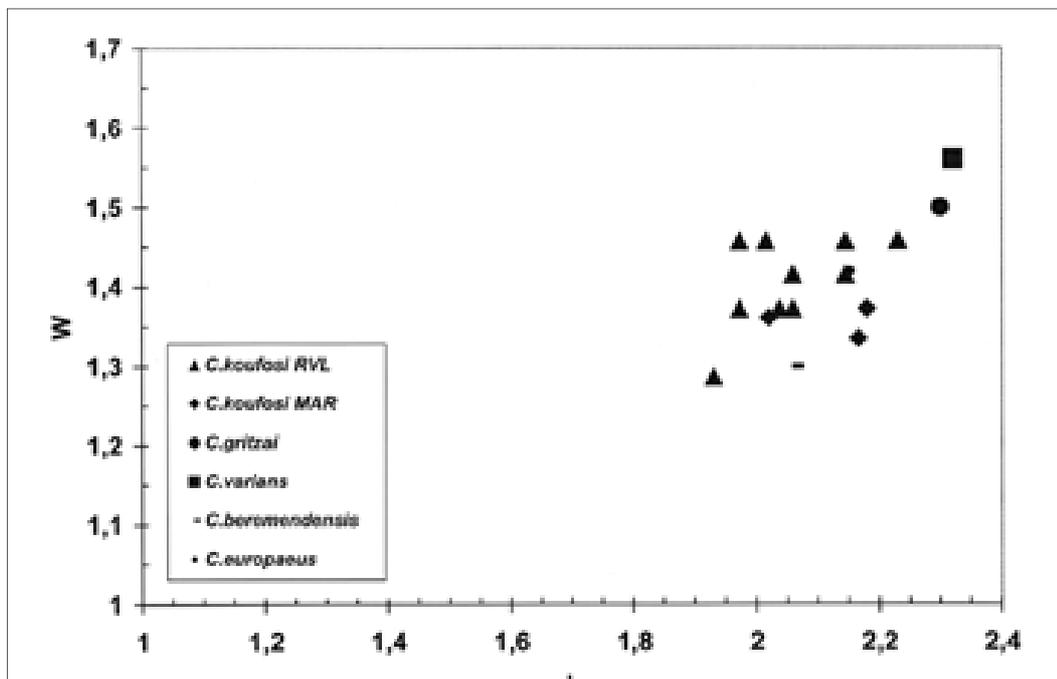


Figure 6 Scatter diagram comparing the dimensions of the M1 of *C. koufosi* from Marathoussa and Ravin Voulgarakis (Koliadimou 1996) and the mean values of *C. gitzai* from Odessa (Topachevski & Sko rik 1992), *C. varians* from Choukoutien (Zheng 1984), *C. beremendensis* from Beremend 15 and *C. europaeus* from Csarnota 2 (Hir 1994).

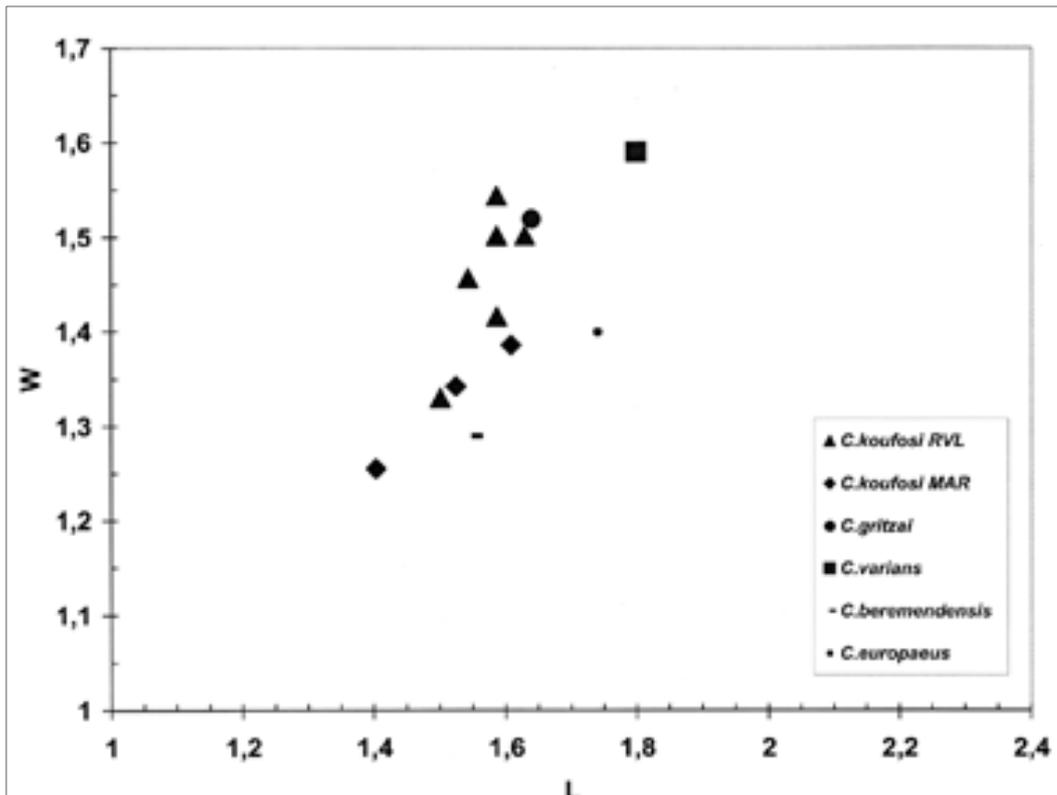


Figure 7 Scatter diagram comparing the dimensions of the M2 of *C. koufysi* from Marathoussa and Ravin Voulgarkis (Koliadimou 1996) and the mean values of *C. gritzai* from Odessa (Topachevski & Sko rik 1992), *C. varians* from Choukoutien (Zheng 1984), *C. beremendensis* from Beremend I5 and *C. europaeus* from Csarnota 2 (Hir 1994).

T3, T4 and the PC. There are no enamel-free areas. The occlusal surface shows three fields: the AL1, the T2 and the rest of the tooth. The enamel-thickness differentiation is of the "*Mimomys*-type". The PC has an almost triangular shape, because of a small salient angle on its lingual side. The synclines are closed at the base of the tooth. The crown-cement is abundant in the LRA2, LRA3, BRA1 and BRA2 and a few in the BRA3. The *linea sinuosa* is in a large distance from the crown, but there are no roots.

Discussion: The material from Marathoussa is scanty. The "*Mimomys*-type" enamel-differentiation, the abundant crown-cement in the synclines, the presence of the *linea sinuosa*

imply that the molars belong to the tribe Arvicolini and, probably, to the genus *Mimomys*. The fact that the synclines close very low and the crown of the teeth is high, lead to the assumption that they belong to a rather advanced species. However, absence of the m1 in the available material makes a comparison with the known *Mimomys* species impossible. The dental features and the size of the teeth are very similar to those of *M. savini* from Ravin Voulgarkis (Koliadimou 1996) and *M. savini* from Monte Peglia (Van der Meulen 1973). However, the limited material does not allow a certain specific determination.

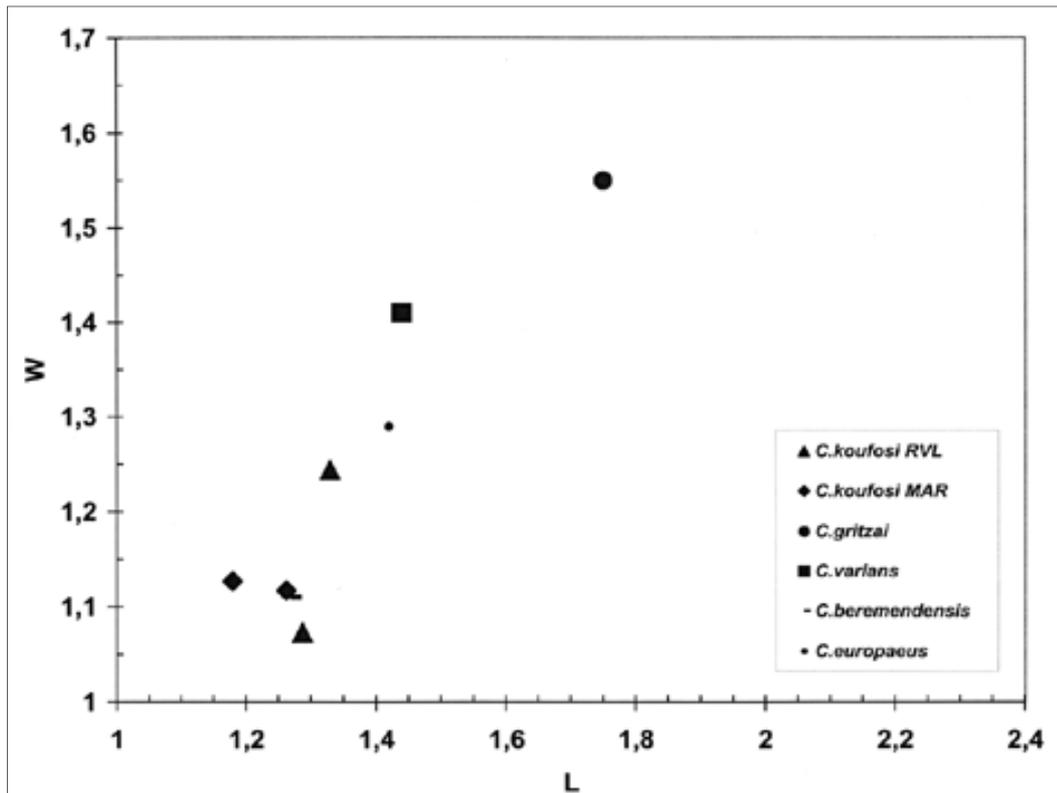


Figure 8 Scatter diagram comparing the dimensions of the M3 of *C. koufosi* from Marathoussa and from Ravin Voulgarakis (Koliadimou 1996) and the mean values of *C. gritzai* from Odessa (Topachevski & Skorik 1992), *C. varians* from Choukoutien (Zheng 1984), *C. beremendensis* from Beremend 15 and *C. europaeus* from Csamota 2 (Hir 1994).

Tribe: Microtini SIMPSON, 1945

Genus: *Microtus* SCHRANK, 1797

Subgenus: *Allophaiomys* KORMOS, 1933

***Microtus (Allophaiomys) pliocaenicus*
(KORMOS, 1933)**

Material:

M1, 15 dex.: 6, 11, 14, 59, 281, 284, 285, 296, 292, 295, 296, 298, 299, 301, 342. 9 sin.: 9, 13, 79, 282, 287, 297, 300, 310, 311.

M2, 14 dex.: 7, 60, 71, 78, 84, 88, 90, 320, 324, 325, 332, 338, 340, 344. 14 sin.: 80, 313, 314, 315, 316, 317, 318, 319, 321, 322, 327, 328, 331, 339.

M3, 15 dex.: 4, 5, 73, 83, 257, 258, 259, 260,

263, 266, 267, 268, 275, 592, 595. 14 sin.: 63, 77, 86, 92, 93, 190, 261, 262, 264, 265, 271, 272, 274, 343.

m1, 13 dex.: 57, 62, 66, 67, 68, 82, 242, 243, 244, 246, 249, 250, 273. 24 sin.: 1, 2, 3, 55, 56, 58, 61, 74, 76, 85, 94, 245, 247, 248, 251, 252, 253, 254, 255, 256, 269, 270, 591.

m2, 7 dex.: 8, 72, 81, 278, 288, 291, 294.

12 sin.: 12, 64, 70, 276, 277, 279, 280, 283, 289, 290, 293, 341.

m3, 14 dex.: 69, 75, 91, 158, 302, 304, 305, 307, 309, 312, 323, 329, 337, 594. 9 sin.: 65, 87, 303, 306, 308, 333, 335, 336, 593.

Measurements: see Tables 19 and 20.

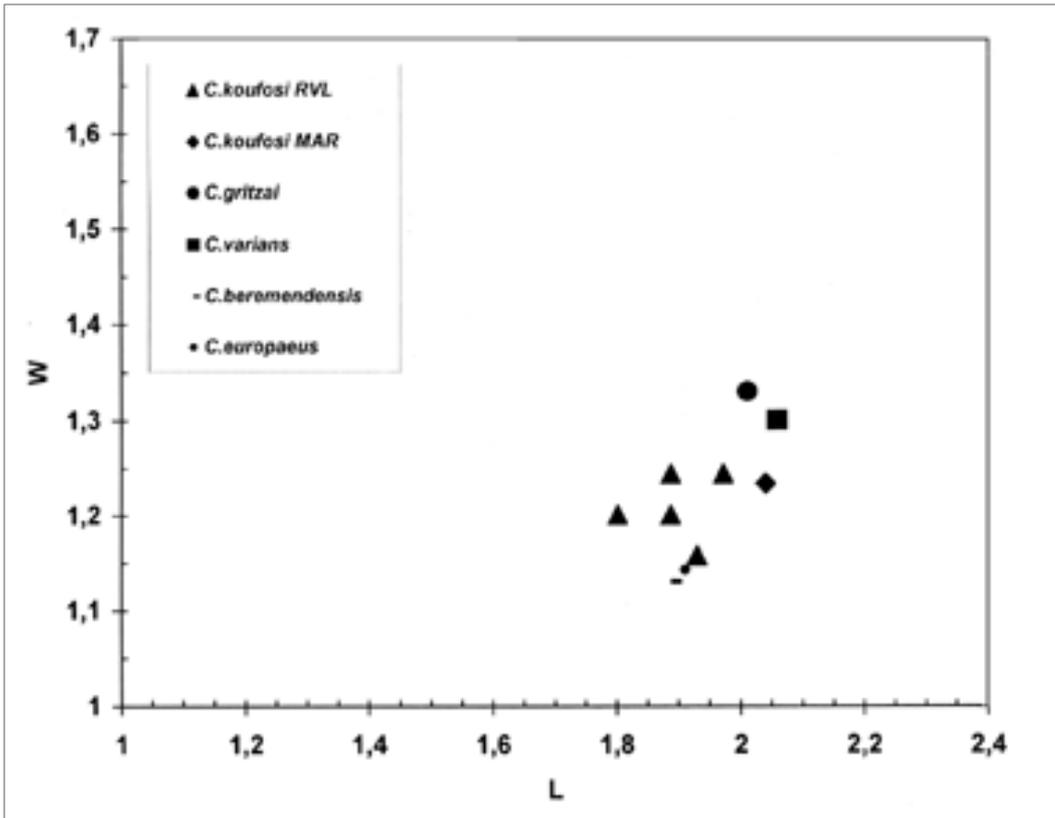


Figure 9 Scatter diagram comparing the dimensions of the m1 of *C. koufosi* from Marathoussa and from Ravin Voulgarakis (Koliadimou 1996) and the mean values of *C. gritzai* from Odessa (Topachevski & Sko rik 1992), *C. varians* from Choukoutien (Zheng 1984), *C. beremendensis* from Beremend 15 and *C. europaeus* from Csarnota 2 (Hir 1994).

Description:

All the upper molars have closed triangles. There is no differentiation of the enamel thickness between the posterior and the anterior part of the anticlines. There is abundant crown-cement in the synclines and there are no roots.

M1: It consists of the AL2, T1, T2, T3 and T4. There are four enamel-free areas: two on both lingual and buccal sides of AL2, one on the buccal side of T1 and one on the posterior part of T4 (in the part of the tooth that contacts to the M2).

M2: It consists of the AL1, T2, T3 and T4. There are three enamel-free areas, two on the two sides of AL1 and one on the posterior

part of T4.

M3 (Plate 5, 6-8): It consists of the AL1, T2, T3, T4, T5 and PC1. There are two lingual and three buccal synclines. The buccal re-entrant angles are shallower than the lingual ones, while the BRA3 is the most shallow and the BRA2 the deepest re-entrant angle. The LRA2 and LRA3 are deep. The occlusal surface shows three fields: in eight specimens the first is AL1, the second T2 and T3 that are confluent and the third the rest of the molar; in one specimen (MAR 93), T2 and T3 are separated, while T3 and PC1 are confluent. In the remaining nineteen specimens there are four fields: the AL1, the T2, the T3 and the rest of the tooth. The buccal anticli-

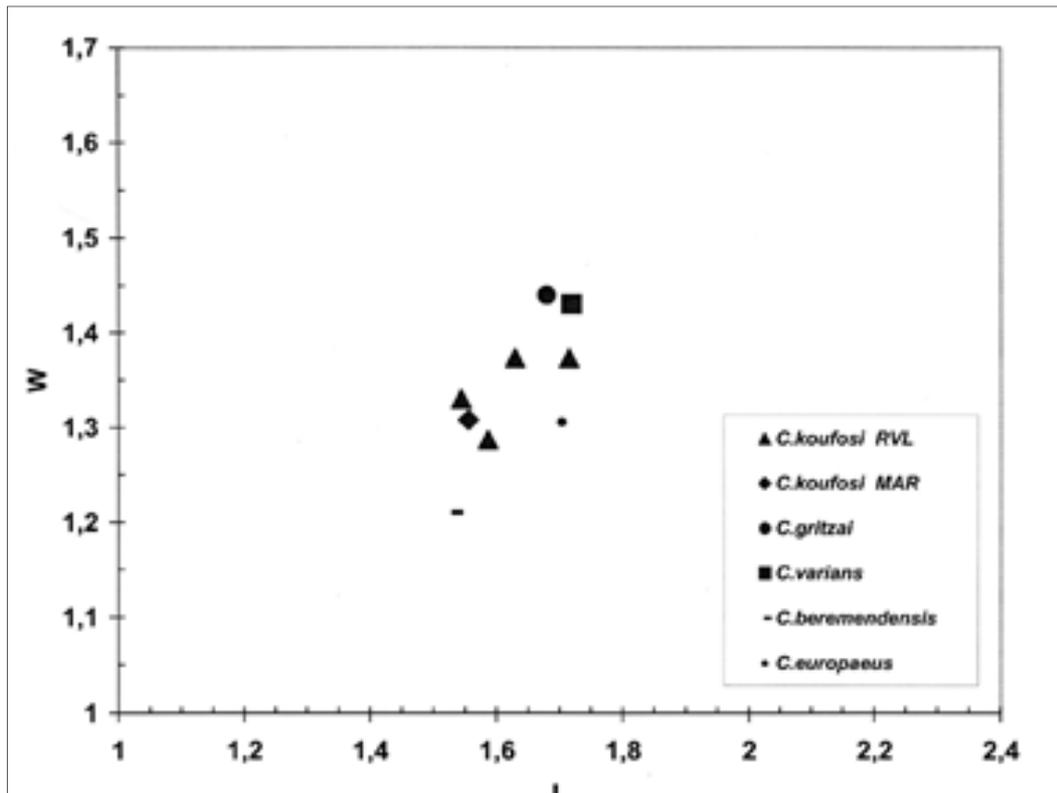


Figure 10 Scatter diagram comparing the dimensions of the m2 of *C. koufosi* from Marathoussa and from Ravin Voulgarakis (Koliadimou 1996) and the mean values of *C. gritzai* from Odessa (Topachevski & Skorik 1992), *C. varians* from Choukoutien (Zheng 1984), *C. beremendensis* from Beremend 15 and *C. europaeus* from Csamota 2 (Hir 1994).

nes are smaller than the lingual ones and less rounded, while the lingual ones are large with rounded ends. The PC is rounded, short and it may bear an incipient lingual re-entrant angle (LRA4). The BRA1, BRA2, LRA2 and LRA3 have always a lot of crown-cement, while BRA3 and the incipient LRA4 (if present) are usually without crown-cement. Only in two out of twenty-four specimens there is crown-cement in the BRA3. In a few specimens the enamel is a little thicker in the posterior part of the anticlines. In the following description of the variability of the posterior cap of the M3, Rabeder's (1981) morphotypes are given in parentheses. Four specimens (18.2 %) have a very simple and rounded PC1, without any trace of BRA3 or LRA4 ("*prosimplex*-type"). One specimen (4.6 %) has a PC1, as above,

but the fields of T2 and T3 are confluent ("*paraprosimplex*-type"). Three specimens (13.6 %) are intermediate between these two types ("*prosimplex-paraprosimplex*-type"). Ten specimens (45.5 %) have a longer PC1 with BRA3, usually with crown-cement, and a LRA4 without crown-cement ("*simplex*-type"). One specimen (4.6 %) is characterised as "*prosimplex-simplex*-type", as it is intermediate between these two types. One other specimen is characterised as "*simplex-para-simplex*-type", because the PC1 is the same as in the "*simplex*-type", but the T2 and the T3 are not completely separated from each other. One specimen has a PC1 with BRA3 and LRA4 with crown-cement and a small LSA5 ("*complex*-type"). Finally, one specimen has a well-developed BRA3, a small

BSA4 and an almost absent LRA4 ("*prae - oeconomus-type*").

All lower molars have thicker enamel in the anterior and central part of the triangles, while it is thinner in the posterior part of the triangles ("*Microtus-type*"). There are no roots.

m1 (Plate 5, 3-5): It consists of the AC2, T5, T4, T3, T2, T1 and PL. There are four lingual and three buccal synclines, all with abundant crown-cement. The occlusal surface shows four fields consisting of the PL, T1, T2 and T3 and one more of the ACC. There are three enamel-free areas: two on each side of the PL and one on the anterior part of the ACC. The morphology of the ACC shows a wide variation and Chaline (1972) distinguished several morphotypes to describe it. Ten specimens (33.3 %) have a very simple AC1 that communicates with the T5 and T4 ("*prehintoni-type*"). Three specimens (10 %) have a more closed and rounded AC1 and a very small T7 starts appearing ("*hintoni-type*"). Twelve specimens (40 %) are intermediate between these two types ("*prehintoni-hintoni-type*"). Two specimens (6.7 %) have a separated, rather elongated AC1, while the T7 is well developed ("*hintoni-gregaloides-type*"). Finally, three specimens (10 %) have a rather elongated AC1 without any sign of T7 ("*laguroides-type*").

m2: It consists of the T4, T3, T2, T1 and PL. There are two lingual and two buccal synclines with abundant crown cement, while in nine specimens there is a little crown cement in front of T3 and in one specimen there is a little crown cement in front of T4. The lingual re-entrant angles are deeper than the buccal ones and the lingual salient angles are bigger than the buccal ones. There are three enamel-free areas: two in each side of the PL and one in the anterior part of T4. The occlusal surface shows four or five fields: PL, T1 and T2 are closed, while in five out of twenty specimens the T3 and T4 communicate with each other and form one field; in the rest (fifteen

specimens) all the fields are closed.

m3: It consists of the T4, T3, T2, T1 and PL. In fifteen specimens there are three dentine fields: the PL, the T1 together with T2 and the T3 together with the T4. In the remaining eight specimens T1 and T2 are closed and only T3 and T4 communicate to a greater or lesser degree. The position of the PL is slightly oblique in relation to the longitudinal axis of the tooth. Other features are as in m2.

Discussion:

The specimens from Marathoussa have abundant crown-cement in the synclines, lacking of roots and enamel-thickness differentiation of the "*Microtus-type*". All these features characterise the genus *Arvicola* of the tribe Arvicolini and all the genera of the tribe Microtini (Koliadimou 1996). However, the teeth of *Arvicola* are much longer and they have more synclines than the specimens from Marathoussa. So, it is obvious that the molars from Marathoussa belong to the tribe Microtini.

We will discuss the m1s and M3s, as the other molars are not diagnostic. The morphology of the ACC of the m1 shows a wide variation and it can be used for specific determination. Three main morphotypes were separated by Van der Meulen (1973), based on the number of the closed triangles in the occlusal surface of the m1. The specimens from Marathoussa belong to the morphotype 1 (AC forms one field): twelve of them (40 %) belong to morphotype 1a (parts of the AC broadly confluent) and eighteen (60 %) to morphotype 1b (narrow connections between the parts of the AC). According to Van der Meulen (1973) morphotype 1 molars characterise the subgenus *Allophaiomys*. In addition to the three main morphotypes, the same author distinguished six additional types of the AC2. The m1s from Marathoussa belong to the following types: "arvicolid-type" 20 % (6 molars), "arvicolid-hintonid-type" 63.3 % (19 molars), "hintonid-type" 6.7 % (2 molars), "arvicolid-ratticepid-type" 10 % (3 molars). The majority of the specimens (90%) belong

to the "arvicolid-hintonid-type" that characterises a primitive species of *Allophaiomys*. Van der Meulen (1973) also proposed the use of three ratios to demonstrate the difference between and the variation of the main morphotypes. These ratios are: A/L, B/W and C/W. The most important ratio is A/L, which expresses the relative length of the AC in comparison to the total length of the molar. It is calculated according to $A/L = a/L * 100$. The frequency distribution of A/L is expected to shift to higher values from older to younger assemblages. Furthermore, he uses the mean values of A/L (M-A/L) to illustrate the increasing length of the AC. The M-A/L for the assemblage from Marathoussa is 43.6 (Table 20), which is only slightly smaller than the same parameter for the assemblage of *Allophaiomys pliocaenicus* from Beftia-2 and Nagyhar-sanyhegy-2 (M-A/L=43.7) (Van der Meulen 1973). The proposed values for M-A/L and M-B/W, by Van der Meulen (1973), for the species *M. (Allophaiomys) pliocaenicus* are: $42.0 = M-A/L < 44.5$ and $23.0 = M-B/W < 28.0$. The values of these parameters of the assemblage from Marathoussa fall within these limits (Table 20, Fig. 11).

According to Chaline's (1972) separation in morphotypes, the specimens from Marathoussa belong to the following morphotypes: "pre-hintoni" 33.3 % (10 molars), "laguroides" 10 % (3 molars), "prehintoni-hintoni" 40 % (12 molars), "hintoni" 10 % (3 molars) and "hintoni-gregaloides" 6.7 % (2 molars). All these morphotypes characterise the subspecies *M. (A.) pliocaenicus laguroides* (KORMOS, 1932), although Chaline (1972) gives for the subspecies a length between 2.12-2.52 (ML=2.30), which is smaller than that of the specimens from Marathoussa (ML=2.624). However, Van der Meulen (1973) and Rabeder (1981) consider the subspecies *M. (A.) pliocaenicus laguroides* to be synonymous to *M. (A.) pliocaenicus pliocaenicus* and, thus, constitute the species *M. (A.) pliocaenicus*.

According to Rabeder (1981), M3s can also

be separated into morphotypes. In the assemblage from Marathoussa, the following types are recognized: "prosimplex" 18.2 % (4 molars), "paraprosimplex" 4.6 % (1 molar), "prosimplex-paraprosimplex" 13.6 % (3 molars), "simplex" 45.5 % (10 molars), "simplex-parasimplex" 4.6 % (1 molar), "complex" 4.6 % (1 molar), and "praeoeconomus" 4.6 % (1 molar). The above morphotypes (except for "complex" and the "praeoeconomus") belong to the *simplex*-Group, which appears to be the most primitive group. The type "complex" belongs to the *complex*-Group and the type "praeoeconomus" to the *oeconomus*-Line, but they represent a very small percentage in the assemblage from Marathoussa. More than 50 % (91 %) of the M3s from Marathoussa belong to the *simplex*-Group and, thus, according to Rabeder (1981), the assemblage belongs to the species *M. (Allophaiomys) pliocaenicus*.

The primitive species *Allophaiomys deucalion* KRETZOI, 1969 is a medium-sized *Microtus* species (Table 21). The three parameters for the m1 are: $M-A/L < 42$ (Fig. 11), $M-B/W = 33$, $M-C/W = 20$. The m1 has a very simple and short ACC and it shows a very broad connection between the AC2 and the triangles T4 and T5 (morphotype 1a of Van der Meulen 1973). The three parameters for the assemblage from Marathoussa sample are not in accordance with the values that are given for this species. Furthermore, the morphology of the ACC is not as simple as that of *A. deucalion*, since almost two thirds of the specimens belong to the type 1b and only one third of them belongs to the type 1a. Because of these reasons, the assemblage from Marathoussa does not belong to the species *A. deucalion*. Since the M-A/L of the Marathoussa m1 is 43.6 (higher than that of *A. deucalion*), it seems that these specimens belong to a younger species.

The species *Allophaiomys chalinei* ALCALDE ET AL., 1981 is a large-sized vole. The enamel in the lower molars is undifferentiated.

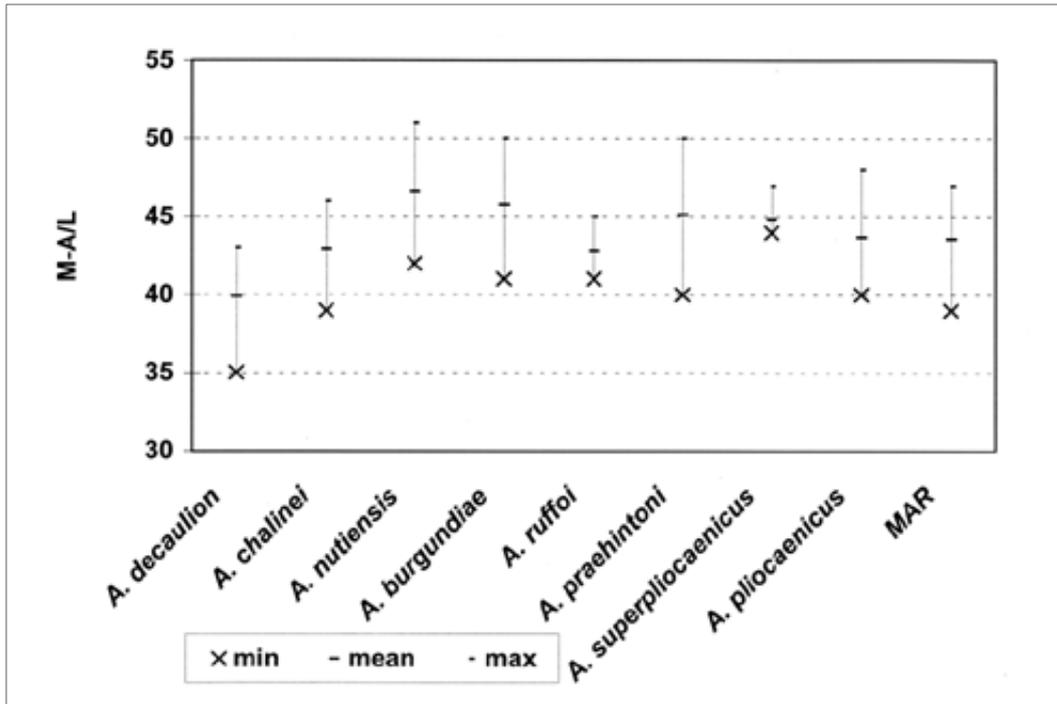


Figure 11 Diagram showing the range of the values and the mean value of the parameter M-A/L for several *Allophaiomys* species (references as on Table 21).

Moreover, the values for the M-A/L are low (Table 21, Fig. 11). The anteroconid complex is very characteristic, with broad and shortened AC1, associated with a very straight anteroconid 'neck', which is reflected in the low value of B/W. On the other hand, the M-C/W reaches high values. Thus, the m1 displays a very accentuated pitomyoid shape, widely confluent T4 and T5 (Van der Meulen & Doukas, in press). The specimens from Marathoussa cannot belong to this species, because their length is much smaller, there is a clear enamel-thickness differentiation, the AC and the T4-T5 are more confluent and the connection between T4 and T5 is narrower. The fact that the value of M-A/L of *A. chalinei* is lower leads to the conclusion that specimens from Marathoussa must belong to a younger species.

The species *A. nutiensis* CHALINE, 1972 (= *Allophaiomys* sp A in Van der Meulen

1973) is a medium-sized vole (Table 21) with elongated and complicated anteroconid complex in m1, showing conspicuous narrowing of the area that connects the AC2 with the T4-T5. The values of the three parameters for the m1s are: $44.5 = M-A/L < 48.5$ (Figure 11), $8.0 < M-B/W = 14.5$, $M-C/W = 20.0$ (Van der Meulen 1973). According to Chaline (1972), the species is characterised by a mixture of morphotypes and the presence of two groups. The first group consists of small-sized m1s, belonging to the morphotypes "*laguroides*", "*plocaenicus*", "*hintoni*" and "*regaloides*". The second group consists of large-sized m1s, belonging to the morphotypes "*preratticepoides*", "*ratticepoides*" and "*nivaloides*". The complete absence of morphotypes of the second group from the Marathoussa sample, as well as the lower value of M-A/L and M-C/W and the higher value of the M-B/W indicate that the specimens from Marathoussa are different and represent a species older than *A. nutiensis*.

The species *A. burgundiae* CHALINE, 1972 (= *Allophaiomys* sp. B in Van der Meulen 1973) is a medium-sized vole (Table 21), with elongated and complicated ACC, usually showing narrowing of the area that connects T4 and T5 and a deep LRA4. The values of the parameters for the m1 are: $44.5 < M-A/L < 46.3$ (Figure 11), $19.5 < M-B/W < 23.0$, $14.0 = M-C/W < 20.0$ (Van der Meulen 1973). The AC2 is usually "nivalid" or "nivalid-ratticepid" (Chaline 1972). These types are absent from the molars from Marathoussa. Furthermore, the value of the M-A/L is lower and the value of the M-B/W is higher than those for *A. burgundiae*. Therefore, the specimens from Marathoussa are distinguished from *A. burgundiae* and it seems that they belong to an older species.

The species *A. ruffoi* PASA, 1947 is a medium to large-sized vole (Table 21). Its m1 has an ACC with narrow connection between T4 and T5. The LRA4 and BRA3 are relatively shallow and, thus, AC2 and the two triangles are confluent. The m1s belong to the "laguroides" and the "preratticepoides" type. The ranges of the three parameters of the *A. ruffoi* assemblage from Cava Sud are: $41 < M-A/L < 45$ (Fig. 11), $19 < M-B/W < 34$ and $12 < M-C/W < 25$ (Van der Meulen & Doukas in press). The mean values of the parameters for the Marathoussa sample are within these limits. However, the dominant morphotype of the m1s from Marathoussa is "prehintoni-hintoni", which is totally absent in *A. ruffoi*. This means that the connection between the AC2 and the T4-T5 is narrower in the specimens from Marathoussa. Furthermore, the mean length of the m1s from Marathoussa is much smaller than that of the m1s of *A. ruffoi*. The specimens from Marathoussa do not belong to *A. ruffoi*, but they are very closely related to it (based on comparisons to a collection of *A. ruffoi* from Cava Sud, Italy, in Utrecht University).

Rabeder (1981) described two new species of

Allophaiomys. *A. praehintoni* is a primitive species with important morphological variability (Table 21). The two dominant morphotypes are "prehintoni" followed by "eoratticeps" (anteroconid complex elongated, confluent T4-T5, very small T7 and LSA5, rather deep LSA4 that prevents wide connection between the AC2 and T4-T5). The value of the M-A/L is between 44.5 and 45 (Fig. 11). In the sample from Marathoussa there are no molars of the "eoratticeps" type and the value of M-A/L is lower than those given for this species.

A. superpliocaenicus is characterised by the presence of the morphotypes "superpliocaenicus", "superlaguroides" and "pliocaenicus", while there are no molars belonging to the "praehintoni" or "hintoni" types (Table 21). Furthermore, the value of the M-A/L is between 44 and 45 (Fig 11) (Rabeder 1981). In the Marathoussa sample there are no specimens belonging to these types and the value of the M-A/L is lower than the minimum value given for this species. Therefore, the studied sample is well distinguished from *A. superpliocaenicus*.

A species of *Microtus* called *M. pitymyoides* has been recognised in the locality Ravin Voulgarakis (RVL) (Koliadimou 1996). The m1s of the assemblage belong to the following types (Chaline's separation, 1972): "prehintoni-hintoni" (7.1 %), "hintoni-gregaloides" (35.8 %), "gregaloides" (9.5 %), "gregaloides-arvaloides" (14.3 %), "arvaloides" (21.4 %), "prenivaloides" (2.3 %), "nivaloides" (4.8 %) and "nivaloides-ratticepoides" (4.8 %). The values of the parameters are: $M-A/L = 48.13$, $M-B/W = 7.38$ and $M-C/W = 20.77$. It is clear that the assemblages from Marathoussa and Ravin Voulgarakis are different. The former assemblage has m1 of the types "prehintoni", "hintoni" and their intermediates, whereas these types are represented in the latter assemblage by a frequency of 7.1 % only. The values of the parameters of the

two assemblages also differ: the value of M-A/L for the Ravin Voulgarakis sample is much higher than that for the Marathoussa sample and the value of M-B/W for the former sample is much lower than that of the latter sample (Table 21). Considering these differences, we can assume that *Microtus pitymyoides* from Ravin Voulgarakis is more advanced than the *Microtus* from Marathoussa.

The species *A. pliocaenicus* is characterised by a simple and short anteroconid complex in the m1, showing no tendency to subdivide. The BRA3 and LRA4 are of equal and considerable depth and the m1s belong mostly to "prehintoni", "hintoni" and their intermediate types. The three parameters have the following values: M-A/L<44.5, M-B/W=23.0 and M-C/W=20.0 (Van der Meulen 1973). All the above features are present in the specimens from Marathoussa and, thus, the sample is determined as *A. pliocaenicus*.

Tribe: Lagurini KRETZOI, 1955

Genus: *Lagurodon* KRETZOI, 1956

***Lagurodon arankae* (KRETZOI, 1954)**

Material:

M1, 3 dex.: 185, 236, 238. 4 sin.: 171, 172, 181, 602.

M2, 4 dex.: 178, 186, 233, 235. 3 sin.: 189, 188, 237.

M3, 4 dex.: 162, 163, 164, 231. 5 sin.: 23, 24, 165, 187, 603.

m1, 8 dex.: 19, 20, 159, 160, 161, 225, 229, 234. 9 sin.: 16, 17, 18, 21, 22, 226, 227, 228, 241.

m2, 7 dex.: 166, 167, 169, 170, 182, 184, 230. 2 sin.: 168, 180.

m3, 4 dex.: 173, 174, 175, 239. 4 sin.: 176, 177, 179, 183.

Measurements: see Table 22.

Description: All the molars have no roots, no crown-cement and the enamel-thickness differentiation is of the "*Microtus*-type"

(thicker on the posterior part of the triangles).

M1: It consists of the AL2, T1, T2, T3 and T4. In four of the studied specimens there is a small anticline, like a beak, in the LRA2. Each triangle constitutes a closed field, without any communication with the other triangles. The enamel-free areas are on the buccal and lingual side of the AL2 and on the posterior edge of T4.

M2: It consists of the AL1, T2, T3 and T4. In six specimens (the seventh is broken) there is a small anticline in the LRA2. The fields on the occlusal surface and the enamel-free areas are as on the M1.

M3 (Plate 5, 9-10): It consists of the AL1, T2, T3, T4 and PC. Among the four specimens that retain the AL1, the two have enamel-free areas on both lingual and buccal side of AL1, while the other two have only one enamel-free area on the lingual side of AL1. The LRA2 is long but without a micro-anticline as on the M1 and M2. The T2 is, in most cases, more developed than the T4. All molars belong to the morphotype "*arankae*" (PC rounded or oval and not very elongated). The molars consist of only one field. One of the molars has a small islet on its PC.

m1 (Plate 5, 11-12): It consists of the PL, T1, T2, T3, T4, T5, T6 and AC1. The fields on the occlusal surface are five: the PL, the T1, the T2, the T3 and the anteroconid complex. The enamel-free areas are on the anterior edge of the AC1, on the buccal side of the T6 and on both the lingual and buccal sides of the PL. Ten specimens (83 %) belong to the morphotype "*arankae*" (BRA4 developed) and two specimens (17 %) to the morphotype "*pannonicus*" (BRA4 almost absent).

m2: It consists of the PL, T1, T2, T3 and T4. Each one of these parts form one field, with very restricted communication among them. The enamel-free areas are on both lingual and buccal sides of the PL and on the anterior edge of the T4.

m3: It consists of the PL, T1, T2, T3 and T4, with very narrow openings from one to the other. The enamel-free areas are as on the m2.

Discussion:

The absence of crown-cement and roots as well as the "Microtus-type" enamel-differentiation indicate the tribe Lagurini. The well developed T6, the absence of a T7, the dominance of the "arankae" morphotype and the presence of four enamel-free areas on the m1, the presence of a micro-anticline in the LRA2 of the M1 and M2 and the dominance of the "arankae" morphotype for the M3 are the dental features that distinguish the assemblage from the genera *Lagurus*, *Prolagurus* and *Eolagurus* and suggest similarities with *Lagurodon* (Koliadimou 1996).

There are two species of *Lagurodon*: *L. arankae* and *L. praepannonicus* (Koliadimou 1996). The m1 of *L. praepannonicus* has an incipient T6, the BRA4 is completely absent and the enamel-free area of the AC expands to the buccal edge of the T6 and, thus, the enamel-free areas of the molar are three (Topachevski 1973). The description of the molars, as given above, agrees with the description of the molars of the species *L. arankae*. The complete absence of m1s of the morphotype "transiens" and the very small representation of the morphotype "pannonicus", both of which are more advanced than the morphotype "arankae", show the rather old age of the material (Koliadimou 1996).

BIOCHRONOLOGY

The micromammalian fauna of Marathoussa includes several species and some of them can help with the dating of the fauna. The Marathoussa fauna consists of the following species: Desmaninae indet., *Crocidura kornfeldi*, *Sorex minutus*, *Sorex (Drepanosorex) praeearaneus*, *Asoriculus gibberodon*, *Beremendia fissidens*, *Spermophilus* sp., *Sicista* cf. *subtilis*, *Apodemus sylvaticus/flavicollis*, *Cricetinus koufosi*, *Mimomys* sp., *Microtus (Allophaiomys) pliocaenicus* and *Lagurodon arankae*.

The insectivores cannot help with the dating of the fauna, as the stratigraphical range of

most of them is quite large (Fig. 12). On the contrary, the rodents of the fauna can give indications for the age of the Marathoussa fauna. The presence of *A. sylvaticus/flavicollis*, *M.(A.)pliocaenicus* and *L. arankae* suggests an Early Biharian age (Fig. 12). Moreover, morphological comparisons for these species allow more definite conclusions. The Marathoussa *Apodemus* represents a form with a mixture of morphological features that are present in the species *A. sylvaticus* and *A. flavicollis*. Both species appeared at the beginning of Pleistocene (Early Biharian) and exist until nowadays. The similarity of the Marathoussa *Apodemus* with that from Ravin Voulgarakis indicates that both faunas are close in age. The latter locality has been dated to Early-Middle Biharian and, more precisely at the Nagyarsanyhegy phase (Koliadimou 1996).

The arvicolid *M.(A.) pliocaenicus* gives more details about the age of the fauna. The First Appearance Datum (FAD) of *Microtus (Allophaiomys)* is considered to mark the end of the Villanyian and the beginning of the Biharian (De Giuli & Torre 1984; Fejfar *et al.* 1997) and this time marker can be used within the Holarctic region (Fejfar & Heinrich 1989). The type locality of *M.(A.) pliocaenicus* is Betfia 2, Romania, dated at the Early Biharian (Van der Meulen 1973). Since then, it has been found in various Eurasian localities (Fig. 12), but it was unknown in Greece. A more detailed comparison of the Marathoussa *Microtus* with other known species provides more biochronological evidences. The parameter M-A/L (as proposed by van der Meulen 1973) for the Marathoussa m1 is only slightly different from those of Betfia 2 and Nagyarsanyhegy 2 (Romania/Hungary), indicating similar age for the three faunas. Moreover, most of the m1 from Betfia 2 and all of them from Nagyarsanyhegy 2 belong to the morphotype 1a (Van der Meulen 1973), while the Marathoussa m1 mainly belong to the morphotype 1b. This suggests a slightly younger

age for Marathoussa than that of the other two sites, which are dated at the Early Biharian (Fig. 12). The presence of a more evolved form of *Microtini* with higher values for the parameter M-A/L in Monte Peglia 63, 11, 12 indicates that Marathoussa is older than the Nagyharsanyhegy phase, at which Monte Peglia is dated. In the locality Ravin Voulgarakis the more evolved species *M. pitymyoides* has been reported. The fauna of Ravin Voulgarakis has been dated at Middle-Late Biharian (Nagyhars-anyhegy phase) (Koliadimou 1996, and Fig. 12). Taking into account all the above mentioned, the Marathoussa fauna is dated at the Early Biharian (Betfia phase) and is slightly younger than Betfia 2 and older than Monte Peglia.

The presence of the species *L. arankae* suggests a possible Early Biharian age for the Marathoussa fauna as well, since the morphotypes for the m1 of the Marathoussa sample are more primitive than those of the Ravin Voulgarakis sample (Koliadimou 1996). Therefore, it is confirmed that the Marathoussa fauna has an Early Biharian age.

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REFERENCES

- Agusti, J., 1990 - The Plio-Pleistocene arvicolid succession in Southern and Eastern Spain - Proceedings of the International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia): 21-32
- Chaline, J., 1972 - Les rongeurs du Pleistocene moyen et supérieur de France (systematique - biostratigraphie - paléoclimatologie) - Cahiers de Paléontologie, Centre National de la Recherche Scientifique, Paris VII
- Daams, R. & Freudenthal, M., 1988 - Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon* - Scripta Geologica, Special Issue 1: 39-132
- De Bruijn, H., 1966 - On the mammalian fauna of the *Hipparion*-Beds in the Calatayud-Teruel basin (Prov. Zaragoza, Spain) IIA, Part II. The Gliridae - Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (B) 69 (3): 1-21
- De Giuli, C. & Torre, D., 1984 - A microfauna with *Allophaiomys pliocaenicus* from Gargano (Southern Italy) - Palaeontographica Italica 73 (n. ser. vol. 43): 129 pp.
- Doukas, C.S., Van den Hoek Ostende, L.W., Theocharopoulos, C.D. & Reumer, J.W.F., 1995 - The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia) - Münchener Geowissenschaftlichen Abhandlungen (A) 28: 43-64
- Engesser, B., 1989 - The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia) - Bollettino della Società Paleontologica Italiana 28 (2-3): 227-252
- Fejfar, O. & Heinrich, W.-D., 1989 - Muroid Rodent Biochronology of the Neogene and Quaternary in Europe - pp. 91-118 in: E. Lindsay, V. Fahlbusch & P. Mein (eds.) - European Neogene Mammal Chronology, Plenum Press, New York
- Fejfar, O., Heinrich, W.-D., Pevzner, M.A. & Vangengeim, E.A., 1997 - Late Cenozoic sequences of mammalian sites in Eurasia: an updated correlation - Palaeogeography, Palaeoclimatology, Palaeoecology 133: 259-288
- Filippucci, M. G., Storch, G. & Macholan, M., 1996 - Taxonomy of the genus *Sylvaemus* in western Anatolia - morphological and electrophoretic

- evidence (Mammalia: Rodentia: Muridae) - *Senckenbergiana biologica* 75 (1/2): 1-14
- Green, M., 1977 - Neogene Zapodidae (Mammalia, Rodentia) from South Dakota - *Journal of Paleontology* 51: 996-1015
- Hir, J., 1994 - *Cricetinus beremendensis* n. sp. (Rodentia, Mammalia) from the Pliocene fauna of Beremend 15 (S. Hungary) - *Fragmenta Mineralogica et Palaeontologica* 17: 71-89
- Hir, J., 1997 - A short sketch of the evolution and stratigraphy of the Plio-Pleistocene cricetids (Rodentia, Mammalia) in Hungary - *Folia Historico Naturalia Musei Matraensis* 22: 43-49
- Koliadimou, K.K., 1996 - Palaeontological and biostratigraphical study of the Neogene/Quaternary micromammals from Mygdonia basin - Ph.D Thesis, University of Thessaloniki (in Greek): 612 pp.
- Kordos, L., 1988 - *Karstocricetus skofleki* gen. n., sp. n. and the evolution of the Late Neogene Cricetidae in the Carpathian Basin - *Fragmenta Mineralogica et Palaeontologica* 13: 65-88
- Kostopoulos, D.S., 1996 - The Plio-Pleistocene Artiodactyls from Macedonia, Greece; systematics, palaeoecology, biochronology - Ph.D Thesis, University of Thessaloniki (in Greek with English summary): 540 pp.
- Kostopoulos, D.S., Vassiliadou, K. & Koufos, G.D., in press - The beginning of Pleistocene in the Balkan area according to the mammal record; palaeozoogeographical approach - *Annales Géologiques des Pays Helléniques*
- Koufos, G.D., Syrides, G.E., Kostopoulos, D.S. & Koliadimou, K.K., 1992 - Apollonia, a new vertebrate site in the Pleistocene of the Mygdonia basin (Macedonia, Greece); the first fossil fresh-water mollusks in the area - *Comptes rendus de l'Académie des Sciences Paris* 315 (II): 1041-1046
- Koufos, G.D., Syrides, G.E., Kostopoulos, D.S. & Koliadimou, K.K., 1995 - Preliminary results about the stratigraphy and the palaeoenvironment of Mygdonia basin, Macedonia, Greece - *Geobios* MS 18: 243-249
- Koufos, G.D. & Kostopoulos, D.S., 1997 - Biochronology and succession of the Plio-Pleistocene macromammalian localities of Greece - *Proceedings Biochrom* 97, Mem. Trav. E.P.H.E., Inst. Montpellier 21: 619-634
- Kretzoi, M., 1959 - A Csarnótai fauna és faunaszint - *A Magyar Allami Földtani Intézet Evi Jelentése az 1959: 297-385*
- Kretzoi, M., 1959 - Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen fauna von Csarnóta im Villányer Gebirge (Südungarn) - *Vertebrata Hungarica* 1: 237-246
- Martin Suárez, E., 1988 - Une nouvelle espèce d'*Apodemus* (Rodentia, Mammalia) du Pliocène de la dépression de Guadix-Baza (Grenade, Espagne) - *Geobios* 21 (1): 523-529
- Martin Suárez, E. & Freudenthal, M., 1993 - Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain) - *Scripta Geologica* 106: 11-34
- Mayhew, D.F., 1977 - Late Pleistocene small mammals from Arnissa (Macedonia, Greece) - *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (B)* 81(3): 302-321
- Mein, P. & Freudenthal, M., 1971 - Les Cricetidae (Mammalia, Rodentia) du Néogène de Vieux-Collonges (Rhône, France). Partie 1: Le genre *Cricetodon* Lartet, 1851 - *Scripta Geologica* 5: 1-51
- Michaux, J. & Pasquier, L., 1974 - Recherche sur les rapports espèce actuelle - espèce fossile chez les Rongeurs du groupe *Apodemus sylvaticus*-*Apodemus flavicollis*. Intéret pour la connaissance de l' Holocène - *Bulletin de la Société Languedocienne de Géographie* 8 (3-4): 381-383
- Montuire, S., Sen, S. & Michaux, J., 1994 - The Middle Pleistocene mammalian fauna from Emirkaya-2, Central Anatolia (Turkey): Systematics and Palaeoenvironment - *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 193 (1): 107-144
- Musser, G.G., Brothers, E.M., Carleton, M.D. & Hutterer, R., 1996 - Taxonomy and distributional records of Oriental and European *Apodemus*, with a review of the *Apodemus-Sylvaemus* problem - *Bonner Zoologische Beiträge* 46 (1-4): 143-190
- Pasquier, L., 1974 - Dynamique évolutive d'un sous-genre de Muridae, *Apodemus (Sylvaemus)*. Etude biométrique des caractères dentaires de populations fossiles et actuelles d'Europe occidentale - These, Université des Sciences et Techniques du Languedoc, Académie de Montpellier.
- Psilovikos, A., 1977 - Palaeogeographic development of Mygdonia valley and the lake (Langada-Volvi area) - Ph.D. Thesis, University of Thessaloniki (in Greek with English summary): 154 pp.
- Rabeder, G., 1981 - Die Arvicoliden (Rodentia,

- Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich - Beiträge zur Paläontologie von Österreich 8: 1-373
- Repenning, C.A., 1967 - Subfamilies and Genera of the Soricidae - Geological Survey Professional Paper 565: 1-73
- Reumer, J.W.F., 1984 - Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary - Scripta Geologica 73: 1-173
- Reumer, J.W.F. & Doukas, C.S., 1985 - Early Pleistocene Insectivora (Mammalia) from Tourkobounia (Athens, Greece) - Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (B) 88 (1): 111-121
- Reumer, J.W.F., 1985 - The generic status and species of *Drepanosorex* reconsidered (Mammalia, Soricidae) - Revue de Paléobiologie 4 (1): 53-58
- Reumer, J.W.F., 1994 - De evolutiebiologie van de spitsmuizen (Mammalia, Insectivora, Soricidae). I. Anatomie, evolutie en biogeografie - Cranium 11 (1): 9-35
- Reumer, J.W.F., 1995 - De evolutiebiologie van de spitsmuizen (Mammalia, Insectivora, Soricidae). II. De subfamilies Crocidosoricinae, Allosoricinae, Limnococinae en Crocidurinae - Cranium 12 (2): 53-63
- Reumer, J.W.F., 1995 - Insectivora (Mammalia: Soricidae, Talpidae) from the Late Pliocene of Frechen, Germany - Deinsea 2: 9-15
- Reumer, J.W.F., 1996 - Quarternary Insectivora (Mammalia) from Southeastern France - Acta Zoologica cracoviensia 39(1): 413-426
- Reumer, J.W.F., 1997 - De evolutiebiologie van de spitsmuizen (Mammalia, Insectivora, Soricidae). III. De subfamilie Soricinae en het literatuuroverzicht - Cranium 15 (1): 13-36
- Rümke, C.G., 1985 - A review of fossil and recent Desmaninae (Talpidae, Insectivora) - Utrecht Micropaleontological Bulletins, Special Publication 4: 1-241
- Schaub, S., 1930 - Quartäre und jungtertiäre Hamster - Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft 49: 1-47
- Tchernov, E., 1968 - A Pleistocene faunule from a karst fissure filling near Jerusalem, Israel - Verhandlungen Naturforschenden Gesellschaft Basel 79 (2): 161-185
- Topachevski, V.A., 1973 - Grizguhi tamanskova Faunisticeskora kompleksa Krimea - Akademia Nauk Ukrainii, C.C.C.P., Naoukova Doumka: 235 pp.
- Topachevski, V.A. & Skorik, A.F., 1992 - Neogenovi i Pleistocenovi nezshie chomiaobrasnie ioga vostochnoi Evropi - Akademia Nauk Ukrainii: 235 pp.
- Van der Meulen, A.J., 1973 - Middle Pleistocene smaller Mammals from the Monte Peglia, (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia) - Quaternaria 17: 1-119
- Van der Meulen, A.J., 1978 - *Microtus* and *Pitymys* (Arvicolidae) from Cumberland Cave, Maryland, with a comparison of some new and old world species - Annals of the Carnegie Museum 47 (6): 101-145
- Van der Meulen, A.J. & Kolfschoten, T. van, 1986 - Review of the Late Turolian to Early Biharian mammal faunas from Greece and Turkey - Mem. Società Geologica Italiana 31: 201-211
- Van de Weerd, A., 1973 - Rodentia from two Pleistocene fissure fillings near Athens - Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen (B) 76 (2): 148-166
- Van de Weerd, A., 1976 - Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfàmbra region, Spain - Utrecht Micropaleontological Bulletins, Special Publication 2: 1-218
- Zheng, S., 1984 - Revised determination of the fossil Cricetine (Rodentia, Mammalia) of Choukoutien district - Vertebrata Palasiatica 22 (3): 179-197

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PLATE I Desmaninae indet. **1:** P4s (MAR 130), occlusal view. **2:** M1d (MAR 35), occlusal view. **3:** M2d (MAR 510), occlusal view. **4:** p4d (MAR 487); **a:** occlusal view, **b:** buccal view. **5:** m1s (MAR 42); **a:** occlusal view, **b:** buccal view. **6:** m3s (MAR 39), occlusal view. *Beremendia fissidens* **7:** P4-M1d (MAR 545), occlusal view. **8:** M2d (MAR 492), occlusal view. **9:** M3s (MAR 531), occlusal view. **10:** m1s (MAR 478); **a:** occlusal view, **b:** buccal view. (Enlargement x20)

PLATE I

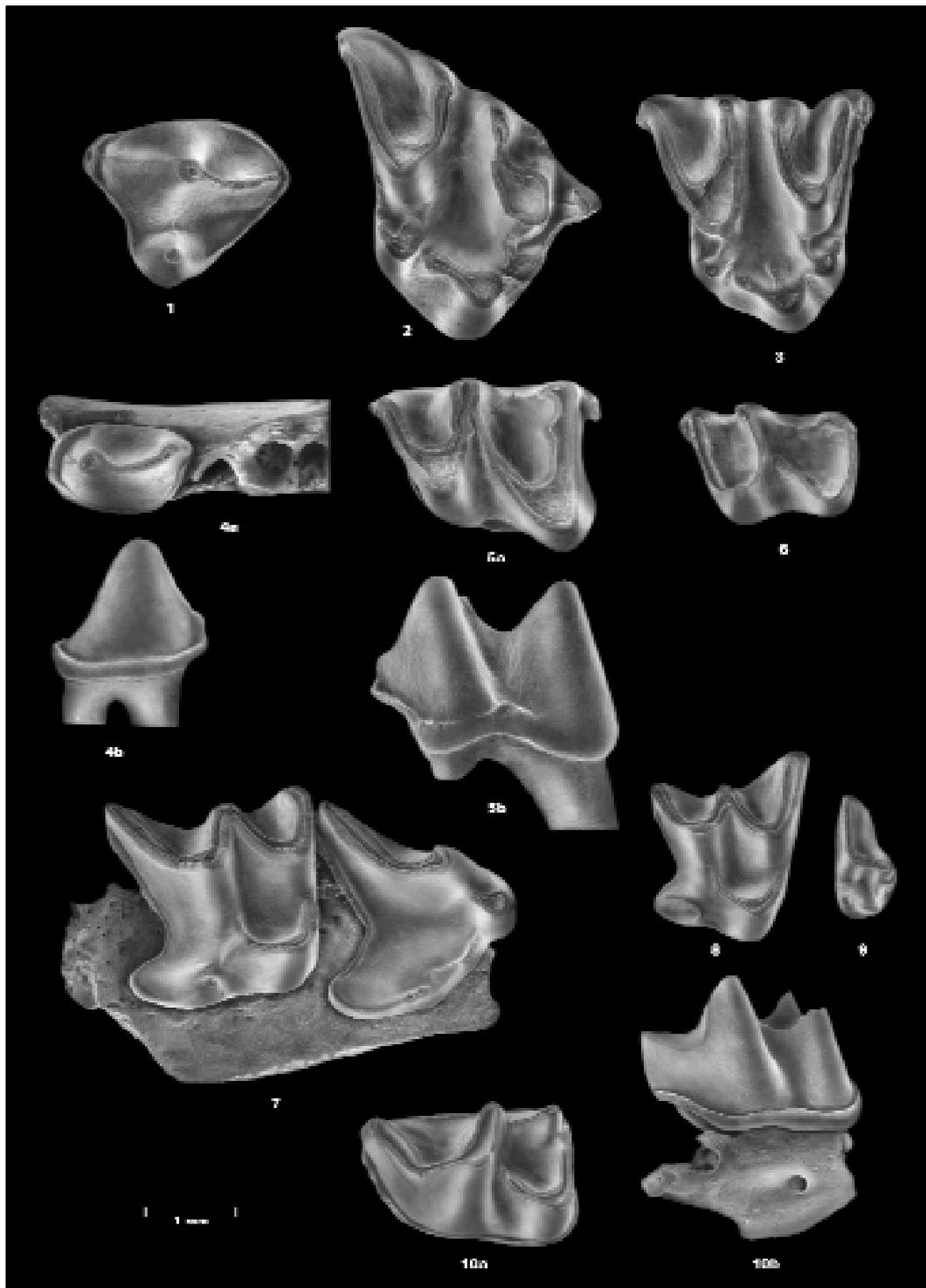


PLATE 2 *Sorex minutus* **1:** Isup s (MAR 32); **a:** buccal view, **b:** occlusal view. **2:** P4s (MAR 89), occlusal view. **3:** M1s (MAR 505), occlusal view. **4:** linf d (MAR 128); **a:** buccal view, **b:** lingual view. **5:** m1s (MAR 107); **a:** occlusal view, **b:** buccal view. **6:** m2d (MAR 443); **a:** occlusal view, **b:** buccal view. *Asoriculus gibberodon* **7:** Isup d (MAR 391); **a:** buccal view, **b:** occlusal view. **8:** M1d (MAR 95), occlusal view. **9:** M2s (MAR 491), occlusal view. **10:** M3d (MAR 534), occlusal view. **11:** linf s (MAR 422); **a:** buccal view, **b:** lingual view. **12:** m1s (MAR 111); **a:** occlusal view, **b:** buccal view. *Crocidura kornfeldi* **13:** Isup s (MAR 429); **a:** buccal view, **b:** occlusal view. **14:** Asup s (MAR 562); **a:** occlusal view, **b:** buccal view. **15:** P4d (MAR 544), occlusal view. **16:** M1d (MAR 544), occlusal view. **17:** M2d (MAR 511), occlusal view. **18:** M3s (MAR 536), occlusal view. **19:** linf s (MAR 412); **a:** buccal view, **b:** lingual view. **20:** p4s (MAR 570), occlusal view. **21:** mandible with m1 and m2 d (MAR 468), buccal view. **22:** m3d (MAR 464); **a:** occlusal view, **b:** buccal view. (Enlargement x20)

PLATE 2

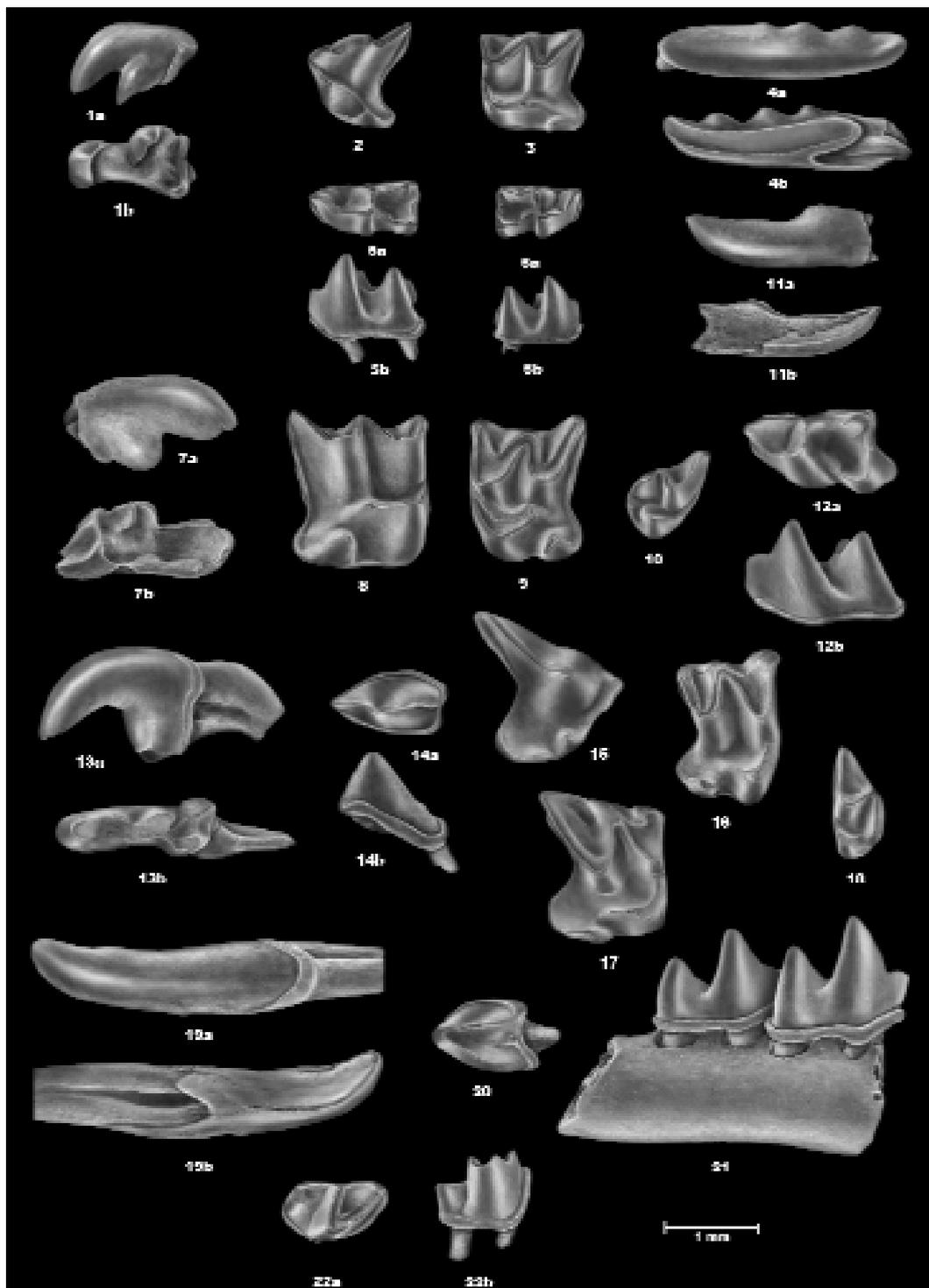


PLATE 3 *Drepanosorex praearaneus* **1**: Isup d (MAR 386); **a**: buccal view, **b**: occlusal view. **2**: Asup d (MAR 601), occlusal view. **3**: P4d (MAR 118), occlusal view. **4**: M1s (MAR 49), occlusal view. **5**: M2d (MAR 97), occlusal view. **6**: M3s (MAR 533), occlusal view. **7**: linf d (MAR 34); **a**: buccal view, **b**: lingual view. **8**: Ainf s (MAR 565); **a**: occlusal view, **b**: buccal view. **9**: p4s (MAR 137); **a**: occlusal view, **b**: buccal view. **10**: mandible with m1, m2 and m3 s (MAR 51); **a**: buccal view, **b**: occlusal view. **11**: ascending ramus with the condyle s (MAR 620); **a**: lingual view, **b**: buccal view. (Enlargement x20)

PLATE 3



PLATE 4

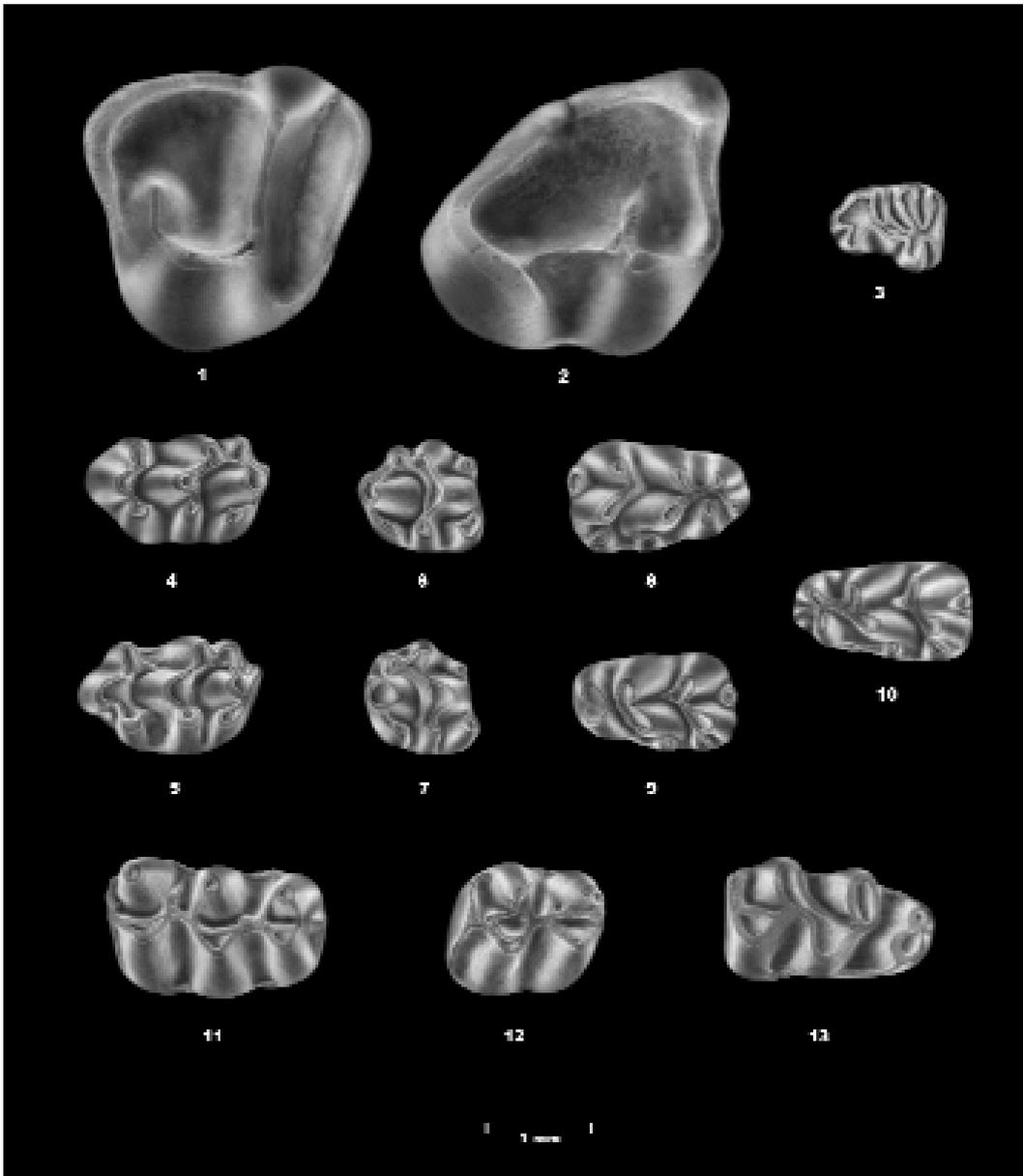


PLATE 4 *Spermophilus* sp. **1:** M1,2d (MAR 378), occlusal view. **2:** m3d (MAR 379), occlusal view. *Sicista* cf. *subtilis*. **3:** m1d (MAR 597), occlusal view. *Apodemus sylvaticus/flavicollis*. **4:** M1s (MAR 196), occlusal view. **5:** M1s (MAR 197), occlusal view. **6:** M2d (MAR 147), occlusal view. **7:** M2d (MAR 199), occlusal view. **8:** m1d (MAR 204), occlusal view. **9:** m1s (MAR 207), occlusal view. **10:** m1s (MAR 209), occlusal view. *Cricetinus koufosi*. **11:** M1d (MAR 345), occlusal view. **12:** M2s (MAR 348), occlusal view. **13:** m1d (MAR 150), occlusal view. (Enlargement x20)

PLATE 5

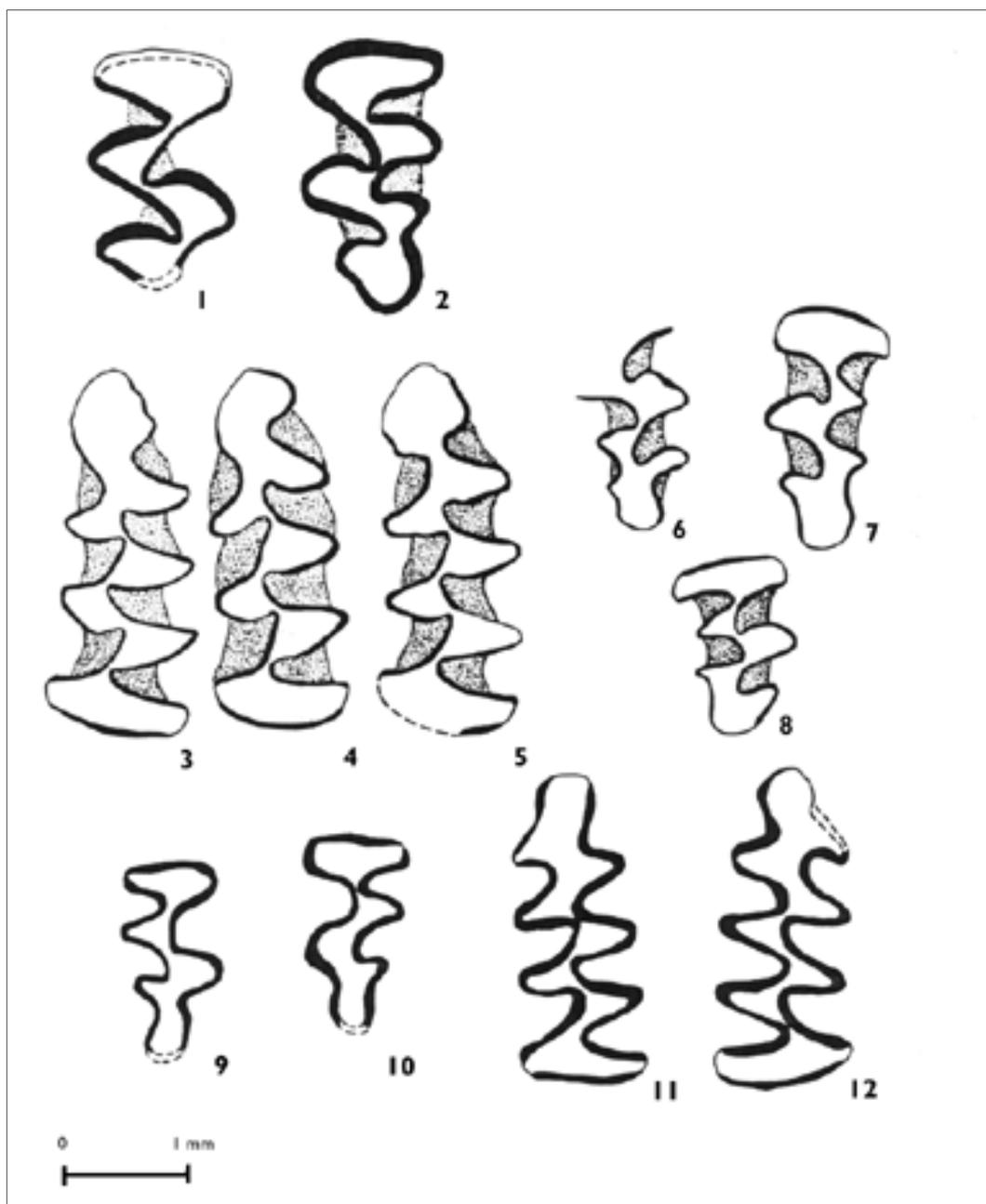


PLATE 5 *Mimomys* sp. **1**: M2s (MAR 240), occlusal view. **2**: M3s (MAR 611), occlusal view. *Microtus (Allophaiomys) pliocaeni* - *cus*. **3**: m1s 'aguroides' type (MAR 248), occlusal view. **4**: m1s 'prehintoni' type (MAR 2), occlusal view. **5**: m1s 'prehintoni-hintoni' type (MAR 251), occlusal view. **6**: M3d 'praeoeconomus' type (MAR 275), occlusal view (fragment). **7**: M3s 'simplex' type (MAR 261), occlusal view. **8**: M3d 'prosimplex' type (MAR 268), occlusal view. *Lagurodon arankae*. **9**: M3d 'arankae' type (MAR 231), occlusal view. **10**: M3s 'arankae' type (MAR 187), occlusal view. **11**: m1s 'arankae' type (MAR 226), occlusal view. **12**: m1d 'arankae' type (MAR 159), occlusal view. (Enlargement x20)

APPENDIX

Table 1 Desmaninae indet., Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper teeth.
(L: length, W: width)

Teeth	Measurement	N	min.	mean	max.
P4	L	1	-	2.353	-
P4	W	1	-	1.949	-
M1	L	2	3.264	3.414	3.564
M1	W	1	-	2.595	-
M2	L	1	-	2.645	-
M2	W	1	-	2.890	-
M3	L	2	1.473	1.542	1.612
M3	W	2	2.018	2.177	2.337

Table 2 Desmaninae indet., Marathoussa (MAR), Macedonia, Greece. Dimensions of the lower teeth.
(TRW: trigonid width, TAW: talonid width)

Teeth	Measurement	N	min.	mean	max.
p2	L	1	-	1.763	-
p2	W	1	-	1.097	-
p3	L	3	1.730	1.811	1.869
p3	W	3	1.050	1.067	1.081
p4	L	1	-	1.851	-
p4	W	1	-	1.167	-
m1	L	1	-	2.670	-
m1	TRW	1	-	1.715	-
m1	TAW	1	-	2.008	-
m2	L	1	-	2.411	-
m2	TRW	1	-	1.744	-
m2	TAW	1	-	1.885	-
m3	L	4	2.087	2.119	2.136
m3	W	3	1.319	1.349	1.404

APPENDIX (continued)Table 3 *C. kornfeldi*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper teeth. (LT: length of the talon, H: height, PE: posterior emargination, LL: lingual length, BL: buccal length, AW: anterior width, PW: posterior width)

Teeth	Measurement	N	min.	mean	max.
I sup	L	6	1.557	1.862	2.009
I sup	LT	10	0.669	0.815	0.917
I sup	H	10	1.080	1.299	1.431
P4	PE	4	0.906	0.942	0.962
P4	LL	4	0.941	0.968	0.995
P4	BL	5	1.720	1.824	1.876
P4	W	4	1.430	1.505	1.639
M1	PE	3	0.954	1.054	1.228
M1	LL	3	1.247	1.381	1.581
M1	BL	3	1.403	1.484	1.555
M1	AW	3	1.707	1.750	1.780
M1	PW	3	1.975	2.033	2.138
M2	PE	5	0.893	1.012	1.092
M2	LL	5	1.153	1.231	1.289
M2	BL	4	1.211	1.278	1.321
M2	AW	3	1.882	1.916	1.970
M2	PW	4	1.677	1.712	1.750
M3	L	1	-	0.608	-
M3	W	1	-	1.299	-

Table 4 *C. kornfeldi*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the lower teeth. (TRW: trigonid width, TAW: talonid width)

Teeth	Measurement	N	min.	mean	max.
I inf	L	1	-	3.171	-
m1	TRW	11	0.867	0.987	0.984
m1	TAW	11	0.929	1.028	1.108
m1	L	11	1.426	1.542	1.644
m2	TRW	4	0.840	0.865	0.906
m2	TAW	4	0.889	0.934	0.995
m2	L	3	1.452	1.474	1.500
m3	L	3	1.158	1.174	1.189
m3	W	3	0.680	0.698	0.722

APPENDIX (continued)Table 5 *Sorex minutus*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper teeth.

Teeth	Measurement	N	min.	mean	max.
I sup	L	8	1.139	1.243	1.409
I sup	LT	8	0.593	0.716	0.809
I sup	H	8	0.726	0.862	0.965
P4	PE	1	-	0.932	-
P4	LL	1	-	1.011	-
P4	Bl	1	-	1.152	-
P4	W	1	-	1.061	-
M1	PE	4	0.912	0.953	0.982
M1	LL	2	1.167	1.179	1.191
M1	BL	4	1.140	1.172	1.190
M1	AW	4	1.126	1.17	1.229
M1	PW	2	1.219	1.292	1.364

Table 6 *Sorex minutus*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the lower teeth.

Teeth	Measurement	N	min.	mean	max.
I inf	L	2	2.570	2.691	2.813
m1	TRW	4	0.584	0.606	0.619
m1	TAW	4	0.660	0.674	0.688
m1	L	4	1.186	1.272	1.333
m2	TRW	7	0.562	0.589	0.624
m2	TAW	7	0.602	0.633	0.662
m2	L	7	1.000	1.165	1.379
m3	L	1	-	0.925	-
m3	W	1	-	0.499	-

APPENDIX (continued)Table 7 *D. praearaneus*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper teeth.

Teeth	Measurement	N	min.	mean	max.
I sup	L	3	1.645	1.831	1.965
I sup	LT	6	0.750	1.045	1.295
I sup	H	6	1.071	1.161	1.334
P4	PE	2	1.084	1.092	1.099
P4	LL	1	-	1.127	-
P4	BL	5	1.478	1.543	1.637
P4	W	1	-	1.472	-
M2	PE	5	1.064	1.092	1.139
M2	LL	5	1.217	1.283	1.362
M2	BL	5	1.196	1.24	1.289
M2	AW	5	1.482	1.561	1.594
M2	PW	5	1.484	1.522	1.567
M3	L	4	0.761	0.802	0.844
M3	W	4	1.221	1.282	1.376

Table 8 *D. praearaneus*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the lower teeth.

Teeth	Measurement	N	min.	mean	max.
I inf	L	2	3.872	3.890	3.908
m1	TRW	6	0.890	0.927	0.964
m1	TAW	6	0.975	1.013	1.051
m1	L	6	1.516	1.624	1.732
m2	TRW	8	0.766	0.861	0.909
m2	TAW	7	0.832	0.904	0.952
m2	L	7	1.409	1.453	1.554
m3	L	5	1.059	1.126	1.163
m3	W	5	0.656	0.694	0.733
m1-m3	L	2	3.800	3.957	4.115

APPENDIX (continued)Table 9 *A. gibberodon*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper teeth.

Teeth	Measurement	N	min.	mean	max.
I sup	L	-	-	-	-
I sup	LT	2	0.660	0.683	0.707
I sup	H	3	1.073	1.142	1.194
M1	PE	3	1.219	1.274	1.317
M1	LL	3	1.410	1.448	1.478
M1	BL	2	1.457	1.508	1.560
M1	AW	3	1.514	1.591	1.669
M1	PW	2	1.566	1.640	1.714
M2	PE	1	-	1.134	-
M2	LL	1	-	1.277	-
M2	BL	1	-	1.313	-
M2	AW	1	-	1.644	-
M2	PW	1	-	1.657	-
M3	L	3	0.722	0.746	0.775
M3	W	3	1.183	1.234	1.278

Table 10 *A. gibberodon*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the lower teeth.

Teeth	Measurement	N	min.	mean	max.
m1	TRW	4	0.797	0.857	0.915
m1	TAW	4	0.965	0.999	1.019
m1	L	4	1.506	1.549	1.602
m2	TRW	2	0.695	0.724	0.753
m2	TAW	2	0.735	0.768	0.800
m2	L	2	1.355	1.366	1.377

APPENDIX (continued)

Table 11 PE-index for the M1s and M2s of morphotype A and B of *A. gibberodon* from various European localities. **1**: Csarnota 2, **2**: Osztramos 7, **3**: Osztramos 9 (Reumer 1984), **4**: Tourkobounia I (Reumer & Doukas 1985), **5**: Marathoussa, **6**: Osztramos I, **7**: Villany 3 (Reumer 1984), **8**: Maramena (Doukas *et al.* 1995).

Locality	morphotype	N (M1)	PE-index (M1)	N (M2)	PE-index (M2)
1	A	51	0.19	43	0.15
2	A	4	0.17	3	0.14
3	A	11	0.22	6	0.21
4	A		0.19		0.16
5	A	2	0.18	1	0.14
2	B	4	0.27	3	0.22
6	B	2	0.26	2	0.24
7	B	1	0.29	-	-
4	B	-	-		0.21
8	B		0.27		0.23

Table 12 Ranges of the dimensions for the lower molars of *A. gibberodon* morphotypes from various localities. **9**: Maritsa (de Bruijn *et al.* 1970) **10**: Apolakkia (Van de Weerd *et al.* 1982). All the other references are as for the Table 11.

<i>A. gibberodon</i>	Loc.	L (m1)	TRW	TAW	L (m2)	TRW	TAW	L (m3)	W(m3)
morphot. A	5	- 16.0	8.6-9.1	- 10.2	13.5- 13.7	6.9- 7.5	7.3-8.0	-	-
	9	- 15.2	7.0-8.0	8.0-9.0	12.5- 13.8	7.0- 8.0	7.2-8.4	10.0- 11.2	5.8-6.5
	10	14.8	7.8	9.1	14.0	7.9	8.2	-	-
Morphot. B	8	13.1 - 15.6	6.8-8.6	7.3-9.3	12.3 - 14.6	6.8- 8.3	7.2-8.6	9.7- 11.1	5.5-5.9
Morphot. A	3	- 15.8	7.2-8.5	7.7-9.4	- 15.6	7.0- 8.0	7.3-8.3	10.2- 11.5	5.6-6.8
Morphot. B	6	- 15.0	7.1-7.6	7.8-8.2	- 14.3	6.2- 7.5	6.7-7.5	- 10.9	5.2-5.8
Morphot. A+B	2	- 18.0	8.1-9.4	8.9- 10.2	- 16.3	7.4- 8.6	7.5-9.1	10.6- 12.4	6.0-6.8
Morphot. A	1	- 17.6	7.0-9.7	8.0- 10.2	- 15.9	6.9- 9.3	7.1-9.2	- 12.3	5.8-7.3
Morphot. B	7	- 15.5	7.8-8.6	8.4-8.8	- 13.8	7.5- 8.2	6.7-8.3	- 11.2	5.6-6.8

APPENDIX (continued)Table 13 *Beremendia fissidens*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the teeth.

Teeth		PE	LL	BL	AW	PW	W	TRW	TAW	L
P4	-	1.49	1.66	2.66	-	-	2.12	-	-	-
M1	min	1.57	2.00	2.32	2.34	2.41	-	-	-	-
M1	max	1.89	2.24	2.33	2.39	2.52	-	-	-	-
M2	-	1.28	1.47	1.71	2.52	1.63	-	-	-	-
M3	-	-	-	-	-	-	1.47	-	-	0.74
M1	-	-	-	-	-	-	-	1.43	1.55	2.61

Table 14 *Spermophilus* sp., Marathoussa (MAR), Macedonia, Greece. Dimensions of the teeth.

Tooth	Measurement	N	min.	mean	max.
M1-2	L	2	2.840	2.858	2.877
M1-2	W	2	2.861	2.950	3.040
m3	L	1	-	2.896	-
m3	W	1	-	2.798	-

Table 15 *Apodemus sylvaticus/flavicollis*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper and lower teeth.

Teeth	Measurement	N	min.	mean	max.
M1	L	11	1.64	1.798	1.90
M1	W	13	1.11	1.212	1.31
M2	L	11	1.12	1.215	1.27
M2	W	11	1.12	1.172	1.24
M3	L	6	0.70	0.758	0.85
M3	W	6	0.76	0.824	0.91
m1	L	10	1.58	1.701	1.77
m1	W	10	0.92	1.029	1.12
m2	L	11	1.12	1.173	1.22
m2	W	11	1.00	1.099	1.21
m3	L	11	0.82	0.898	1.04
m3	W	11	0.78	0.832	0.96

APPENDIX (continued)

Table 16 Mean values of M1 and m1 dimensions of various *Apodemus* species. *A. dominans* (de Bruijn & Van der Meulen 1975), *A. caesareanus* (Tchernov 1968), *A. levantinus* (Tchernov 1968), *A. etruscus* (Engesser 1989), *A. atavus* (Fejfar & Storch 1990).

<i>Apodemus</i> species	Locality	M-L of M1	M-W of M1	M-L of m1	M-W of m1
<i>sylvat./flavic</i>	Marathoussa	1.798	1.212	1.701	1.290
<i>dominans</i>	Tourkovounia 1	2.001	1.294	1.880	1.097
<i>caesareanus</i>	Deblais, Israel	1.917	-	1.729	-
<i>levantinus</i>	Deblais, Israel	2.100	1.270	1.966	1.250
<i>etruscus</i>	Maremma, Italy	1.995	1.210	1.790	1.040
<i>atavus</i>	Gundersheim 4, Germany	1.840	1.200	1.770	1.060

Table 17. Mean values of M1 and m1 dimensions of *A. sylvaticus* and *A. flavicollis* from several localities and different ages:

1: Camargue, France (Pasquier 1974), **2:** Kebara Cave, Israel (Tchernov 1968), **3:** Belvédère 3, the Netherlands (Van Kolfshoten 1985), **4:** Le Lazaret, France (Pasquier 1974), **5:** Monte Peglia 63, Italy (Van der Meulen 1973), **6:** Ravin Voulgarakis, Greece (Koliadimou 1996), **7:** Kirchdorf, Austria (Pasquier 1974), **8:** Gondrenans, France (Pasquier 1974), **9:** Pirro Nord 1, Italy (De Giuli & Torre 1984), **10:** Tourkobounia 2, Greece (Van der Meulen in press), **11:** Amissa, Greece (Mayhew 1977), **12:** Varkiza 2, Greece (Van de Weerd 1973).

<i>Apodemus</i> species	Age	M-L of M1	M-W of M1	M-L of m1	M-W of m1
<i>sylvaticus</i> (1)	recent	1.79	1.24	1.72	1.10
cf. <i>sylvaticus</i> (2)	Up.Pleistocene	1.70	1.10	-	-
<i>sylvaticus</i> (3)	Mid.Pleistocene	1.93	1.20	1.84	1.08
<i>sylvaticus</i> (4)	Mid.Pleistocene	2.10	1.36	1.90	1.17
cf. <i>sylvaticus</i> (5)	Low Pleistocene	1.75	1.10	1.65	0.98
cf. <i>sylvaticus</i> (6)	Low Pleistocene	1.89	1.22	1.70	1.05
<i>flavicollis</i> (7)	recent	1.94	1.26	1.80	1.11
<i>flavicollis</i> (8)	Up.Pleistocene	1.94	1.30	1.84	1.05
<i>flavicollis</i> (9)	Low Pleistocene	2.05	1.34	1.88	1.14
cf. <i>flavicollis</i> (10)	Low Pleistocene	1.95	1.25	1.80	1.11
<i>Apodem. sp</i> (11)	Up.Pleistocene	1.82	1.18	1.84	1.09
<i>Apodem. sp</i> (12)	M-Up.Pleistoc.	2.10	1.33	-	-
<i>sylv/flavic.</i> (MAR)		1.80	1.21	1.70	1.03

APPENDIX (continued)Table 18 *C. cf. koufosi*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper and lower teeth.

Teeth	Measurement	N	min.	mean	max.
M1	L	3	2.020	2.122	2.180
M1	W	3	1.335	1.356	1.373
M2	L	3	1.404	1.513	1.609
M2	W	3	1.255	1.328	1.386
M3	L	2	1.180	1.221	1.263
M3	W	2	1.117	1.122	1.127
m1	L	1	-	2.041	-
m1	W	1	-	1.234	-
m2	L	1	-	1.556	-
m2	W	2	1.308	1.360	1.412

Table 19 *Microtus (Allophaiomys) pliocaenicus*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper and lower teeth.

Teeth	Measurement	N	min.	mean	max.
M1	L	15	1.893	2.565	2.254
M1	W	15	1.015	1.346	1.224
M2	L	19	1.537	1.926	1.724
M2	W	16	0.896	1.133	1.041
M3	L	13	1.380	1.860	1.715
M3	W	13	0.832	0.999	0.920
m1	L	14	2.386	2.818	2.624
m1	W	24	0.731	1.033	0.855
m2	L	11	1.504	1.653	1.594
m2	W	12	0.937	1.108	0.980
m3	L	11	1.270	1.588	1.431
m3	W	11	0.718	0.948	0.831

Table 20 Statistical parameters for the m1 of *M. pliocaenicus* from Marathoussa.

Parameter	N	min.	mean	max.
A/L*100	14	39.492	M-a/l=43.6	47.344
B/W*100	24	11.436	M-B/W=24.6	42.724
C/W*100	24	6.047	M-C/W=18.5	37.101

APPENDIX (continued)Table 21 The statistical parameters of the mIs of the species of *Allophaiomys* from several localities. **1, 3, 4, 8:** Van der Meulen (1973); **2, 5:** Van der Meulen & Doukas (in press); **6, 7:** Rabeder (1981); **10:** Koliadimou (1996).

<i>Microtus</i> species	Locality	N	mean L	Range of A/L (M-A/L)	Range of B/W (M-B/W)	Range of C/W (M-C/W)
1. <i>deucalion</i>	Villani-5	16	2.747	35-43 (39.9)	30-50 (36.8)	15-34 (24.6)
2. <i>chalconi</i>	Cueva Victoria	16	3.030	39-46 (42.9)	05-40 (16.9)	13-30 (21.1)
3. <i>nutiensis</i>	Monte Peglia63	104	2.581	42-51 (46.6)	05-33 (13.9)	06-37 (22.4)
4. <i>burgundiae</i>	Monte Peglia3	76	2.751	41-50 (45.8)	06-33 (21.2)	05-28 (17.4)
5. <i>ruffoi</i>	Cava Sud	9	2.804	41-45 (42.8)	19-34 (25.9)	12-25 (19.7)
6. <i>praehintoni</i>	Deutsch-Altenburg	200	2.680	40-50 (45.14)		
7. <i>superpliocaenicus</i>	Deutsch-Altenburg	10	2.490	44-47 (44.8)		
8. <i>pliocaenicus</i>	Betfia-2	96	2.651	40-48 (43.7)	08-35 (25.3)	15-30 (22.0)
9. <i>pliocaenicus</i>	MAR	14	2.624	39-47 (43.6)	11-23 (24.6)	06-37 (18.5)
10. <i>pitymyoides</i>	RVL	29	2.673	42-51 (48.1)	4-29 (7.38)	9-30 (20.8)

APPENDIX (continued)Table 22 *Lagurodon arankae*, Marathoussa (MAR), Macedonia, Greece. Dimensions of the upper and lower teeth.

Tooth	Measurement	N	min.	mean	max
M1	L	1	-	2.112	-
M1	W	1	-	1.148	-
M2	L	4	1.537	1.667	1.759
M2	W	4	0.875	0.938	1.033
M3	L	4	1.413	1.508	1.545
M3	W	4	0.753	0.808	0.858
m1	L	2	2.378	2.422	2.466
m1	W	2	1.032	1.041	1.049
m2	L	7	1.306	1.458	1.548
m2	W	7	0.720	0.838	0.908
m3	L	3	1.472	1.537	1.639
m3	W	3	0.656	0.712	0.753